PHYLOGENETIC STUDIES ON DIDELPHID MARSUPIALS II. NONMOLECULAR DATA AND NEW IRBP SEQUENCES: SEPARATE AND COMBINED ANALYSES OF DIDELPHINE RELATIONSHIPS WITH DENSER TAXON SAMPLING

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ABSTRACT

In order to test the results of a previous study of didelphid marsupial phylogeny based on IRBP nuclear gene sequences (Jansa and Voss, 2000. Phylogenetic studies on didelphid marsupials I. Introduction and preliminary results from nuclear IRBP gene sequences. Journal of Mammalian Evolution 7: 43–77), we surveyed external, cranial, dental, and karyotypic characters among a more densely taxon-sampled didelphine ingroup. Separate maximum-parsimony analyses of these nonmolecular data and of a new (taxon-dense) IRBP matrix yielded superficially dissimilar strict-consensus topologies. However, no didelphine clade that was even moderately well supported by either separate analysis was contradicted by any equivalently well-supported clade in the other. Instead, all examples of taxonomic incongruence involved weak nodal support from one or both datasets. A maximum-likelihood analysis of the IRBP data produced a consensus topology that was completely congruent with, although slightly more resolved than, the maximum-parsimony consensus. A combined (simultaneous) maximum-parsimony analysis of both datasets (nonmolecular + IRBP) produced a consensus topology that closely resembled the results of analyzing IRBP separately. Most of the didelphine relationships previously reported by Jansa and Voss (op. cit.) are supported by these analytic exercises, with some notable exceptions. The taxon currently known as *Marmosa canescens* is conspicuously divergent from congeneric species and variously clusters with three different groups ("other *Marmosa*" + *Micoureus, Monodelphis,* or higher didelphines [= clade H of Jansa and Voss, op. cit.]) in several parsimony-equivalent resolutions of a fourfold basal polytomy in the IRBP and combined-data consensus topologies. Even without *canescens,* however, the genus *Marmosa* is not demonstrably monophyletic. The nomenclatural consequences of these results are discussed, and a new genus is described for "*Marmosa*" *canescens.* Future analyses should test the monophyly of other speciose didelphine genera, but new sources of character data will be needed to offset the loss of resolution and decreased nodal support that are often caused by denser taxon sampling.

INTRODUCTION

Didelphids are morphologically primitive marsupials whose extant crown group (table 1) is widely distributed in temperate and tropical habitats of the New World. Didelphids have long been of interest to mammalian biogeographers as the most diverse surviving lineage of the old endemic fauna that evolved in South America throughout the long Tertiary isolation of that continent from neighboring land masses, and as the only substantially intact radiation of metatherian mammals outside Australasia (Simpson, 1971; Patterson and Pascual, 1972; Marshall, 1982). Didelphids have been considered living exemplars of plesiomorphic or "generalized" therians by many experimental researchers (e.g., Crompton and Hiiemae, 1970; Jenkins, 1971; Jerison, 1973; Silveira et al., 1982; Harder, 1992; Frost and Masterton, 1994; Bedford, 1996), whereas comparative biologists have studied morphological, behavioral, and physiological variation among didelphids to test adaptive hypotheses about the evolution of convergent traits among placental mammals (e.g., McNab, 1978; Eisenberg and Wilson, 1981; Charles-Dominique, 1983; Grand, 1983; Lemelin, 1999). By contrast with the modest literature resulting from these more-or-less traditional motivations for didelphid research, the recent popularity of *Monodelphis* and *Didelphis* as model organisms for biomedical investigations has resulted in hundreds of papers on topics ranging from oncology to central nervous system regeneration following trauma (see reviews by VandeBerg, 1990; Archer et al., 1997; Krause et al., 1997; Martin and Wang, 1997; VandeBerg and Robinson, 1997).

Unfortunately, advances in didelphid phylogenetics have not kept pace with the burgeoning potential for innovative research based on recent biomedical discoveries. For example, traits that are now regarded as uniquely valuable attributes of model didelphid species—such as the ability of *Didelphis virginiana* blood proteins to detoxify snake venom and other organic poisons (Catanese and Kress, 1993; Thwin and Gopalakrishnakone, 1998; Lipps, 1999) or the susceptibility of *Monodelphis domestica* to melanoma induction by ultraviolet radiation (Ley, 1991; Kusewitt et al., 2000; Ley et al.,

TABLE 1
Composition of the Didelphid Crown Group[a]

- Caluromyinae
  - *Caluromys* (3 spp.)
  - *Caluromysiops* (1 sp.)
  - *Glironia* (1 sp.)
- Didelphinae
  - "Marmosines"
    - *Gracilinanus* (7 spp.)[b]
    - *Lestodelphys* (1 sp.)
    - *Marmosa* (10 spp.)[c]
    - *Marmosops* (14 spp.)[d]
    - *Micoureus* (4 spp.)[e]
    - *Thylamys* (8 spp.)[f]
  - "Large $2n = 22$ opossums"
    - *Chironectes* (1 sp.)
    - *Didelphis* (6 spp.)[g]
    - *Lutreolina* (1 sp.)
    - *Philander* (4 spp.)[h]
  - Others
    - *Metachirus* (1 sp.)
    - *Monodelphis* (17 spp.)[i]
- Incertae sedis
  - *Hyladelphys* (1 sp.)[j]

[a]Subfamilial contents, generic taxonomy, and species counts are from Gardner (1993) except as noted. Only Recent genera and species are tabulated. "Marmosines" are small didelphines formerly included in or allied with *Marmosa* (sensu Tate, 1933). "Large $2n = 22$ opossums" are widely recognized as a group based on body size and karyotype. "Others" are didelphines of traditionally uncertain relationships.

[b]Including *Gracilinanus perijae* Hershkovitz (1992b), but excluding two other species described as new in the same publication: "*G.*" *kalinowskii* (transferred to *Hyladelphys* by Voss et al., 2001) and *G. longicaudus* (synonymized with *G. emiliae* by Voss et al., 2001).

[c]Including *Marmosa quichua* (a synonym of *M. murina* according to Gardner, 1993) but recognized as distinct by Voss et al. (2001) after Tate (1933).

[d]Including *Marmosops bishopi*, *M. juninensis*, and *M. pinheiroi* (formerly synonymized with *M. parvidens*; see Voss et al., 2001); *M. neblina* (formerly synonymized with *M. impavidus*; see Patton et al., 2000); and *M. paulensis* (formerly synonymized with *M. incanus*; see Mustrangi and Patton, 1997).

[e]Including *Micoureus paraguayanus* (formerly synonymized with *M. demerarae*; see appendix 3).

[f]Including *Thylamys cinderella*, *T. sponsoria*, and *T. venustus* (formerly synonymized with *T. elegans*; see Flores et al., 2000).

[g]Including two former synonyms of *Didelphis albiventris*: *D. imperfecta* and *D. pernigra* (see Lemos and Cerqueira, 2002).

[h]Including *Philander mcilhennyi* and *P. frenata* (formerly synonymized with *P. andersoni* and *P. opossum*, respectively; see Patton and da Silva, 1997).

[i]Including *Monodelphis glirina* and *M. palliolata* (formerly synonymized with *M. brevicaudata*; see Voss et al., 2001).

[j]Named by Voss et al. (2001) to contain *Hyladelphys kalinowskii*, originally described as a species of *Gracilinanus* by Hershkovitz (1992b).

2000)—presumably had evolutionary precursors that may persist in sister lineages from which the stepwise accumulation of relevant mutations could be reconstructed if a phylogeny were available. To date, however, progress in inferring didelphid evolutionary history has been limited.

The history of phylogenetic research with Recent didelphids was reviewed in our first report (Jansa and Voss, 2000), which discussed and illustrated the results of several landmark studies including Creighton's (1984) and Reig et al.'s (1987) parsimony analyses of nonmolecular (mostly morphological) characters, Kirsch and Palma's (1995) distance analyses of scnDNA hybridization data, and Patton et al.'s (1996) parsimony analyses of mtDNA sequences. To summarize briefly, the monophyly of only one suprageneric grouping—a clade of large-bodied opossums with $2n = 22$ chromosomes (*Chironectes*, *Didelphis*, *Lutreolina*, *Philander*)—is consistent with the published results of all four analyses. Some additional relationships, however, were supported by a simple majority of those studies that included appropriate generic exemplars, including (1) monophyly of the subfamily Didelphinae, (2) monophyly of a group consisting of species of *Marmosa* and *Micoureus*, (3) a sister-group relationship of *Thylamys* with *Lestodelphys*, and (4) a sister-group relationship of *Metachirus* with the large-bodied $2n = 22$ clade. Palma and Spotorno's subsequent (1999) analysis of mitochondrial 12S rRNA sequences (not reviewed by Jansa and Voss, 2000) provided additional support for the monophyly of Didelphinae, of the large $2n = 22$ opossums, and of *Marmosa* + *Micoureus*, but not for the sister-group relationship of *Metachirus* with the large-bodied $2n = 22$ clade. Most of the taxa with conspicuously incongruent or unresolved relationships as indicated by these aggregate results are didelphines, notably *Gracilinanus*, *Marmosops*, *Metachirus*, and *Monodelphis*.

The causes of incongruence among past analyses of didelphid phylogeny are hard to identify with certainty (Jansa and Voss, 2000), but they plausibly include disparate taxon sampling (no two studies have analyzed relationships among the same set of taxa); use of nonmonophyletic supraspecific

taxa as analytic terminals; discrepant scoring of the same characters in different morphological studies; different rooting criteria (outgroups versus reconstructed ancestors); and voucher misidentifications or tissue/voucher mismatches. Sampling error in resolving relationships is also implicated by the low bootstrap support for many nodes in those studies that reported such statistics (Patton et al., 1996; Palma and Spotorno, 1999).

To address these and other problems, we (Jansa and Voss, 2000) analyzed 548 parsimony-informative characters obtained by sequencing 1158 bp of the first protein-coding region (exon 1) of the nuclear IRBP gene[1] for 21 didelphid terminals representing all then-recognized genera. Previously published IRBP sequences from nondidelphid marsupials were included to test didelphid monophyly, and multiple placental sequences were included as outgroups (marsupial monophyly was assumed). The resulting tree (fig. 1) was almost completely resolved and provided strong support for (1) a sister-group relationship between *Caluromys* and *Caluromysiops*; (2) monophyly of Didelphinae; (3) monophyly of a *Marmosa* group that includes *Micoureus*; (4) a sister-group relationship between *Monodelphis* and the *Marmosa* + *Micoureus* complex; (5) a group including *Thylamys*, *Lestodelphys*, and *Gracilinanus*; (6) a sister-group relationship between *Marmosops* and the *Thylamys* group; (7) monophyly of the large $2n = 22$ opossums; and (8) a sister-group relationship between *Metachirus* and the large $2n = 22$ clade.

Node-by-node comparisons of these results with previously published phylogenetic hypotheses suggested that most examples of conflict do not reflect substantial data incongruence (Jansa and Voss, 2000). Nevertheless, the striking lack of agreement between our tree and phylogenies or classifications resulting from various nonmolecular studies (e.g., Creighton, 1984; Reig et al., 1987; Hershkovitz, 1992b; Goin and Rey, 1997) indicates the need for a critical reassessment of the morphological and karyotypic characters on which those hierarchies were based. Plausibly, some traditionally recognized groupings could have resulted from misinterpreted homologies, problematic polarity assessments, or inappropriate assumptions about evolutionary processes. Alternatively, nonmolecular data might provide compelling evidence for relationships that are not or are only weakly supported by our molecular results.

Taxon sampling is another concern, because our IRBP dataset included only a small fraction—about 25%—of extant didelphid diversity at the species level. Denser sampling in the neighborhood of problematic nodes where traditional generic distinctions are not supported by sequence data (e.g., *Didelphis* versus *Philander*; fig. 1) is a clear priority. In addition, because didelphid taxonomy has not been revised for many years, it is possible that highly divergent clades remain to be discovered within speciose genera hitherto recognized on the basis of traditional (subjective) criteria. Lastly, enlarging our dataset to include type species and other nomenclaturally important taxa is essential to confidently associate analytic results with appropriate clade names.

In this report we describe nonmolecular character variation among 35 didelphid species, including all of those previously sequenced for IRBP exon 1 and others chosen to supplement the taxon sampling of our first study. In compiling these data, we evaluated all of the integumental and craniodental characters analyzed by previous students of didelphid phylogeny in addition to new characters not considered in earlier studies. To provide a comparably taxon-dense molecular dataset, we sequenced 28 new specimens (totalling 32.4 kb) for this report. Below, we analyze our nonmolecular and sequence data separately and in combination to explore patterns of character congruence and conflict between these traditionally recognized categories of taxonomic variation.

[1] The Interphotoreceptor Retinoid Binding Protein (also known as the Interstitial Retinol Binding Protein) is encoded by a single-copy nuclear DNA sequence and is found in all vertebrate eyes, where it apparently functions in the transfer of retinoids during light- and dark-phase adaptation (Bridges et al., 1986; Fong et al., 1990; Pepperberg et al., 1993). Sequence data from IRBP exon 1 were first used phylogenetically to address relationships among mammalian orders (Stanhope et al., 1992, 1996; Springer et al., 1997, 1999; Gatesy et al., 1999), but have also been analyzed at lower taxonomic levels (Yoder and Irwin, 1999; Suzuki et al., 2000; Jansa and Voss, 2000; Michaux et al., 2002).

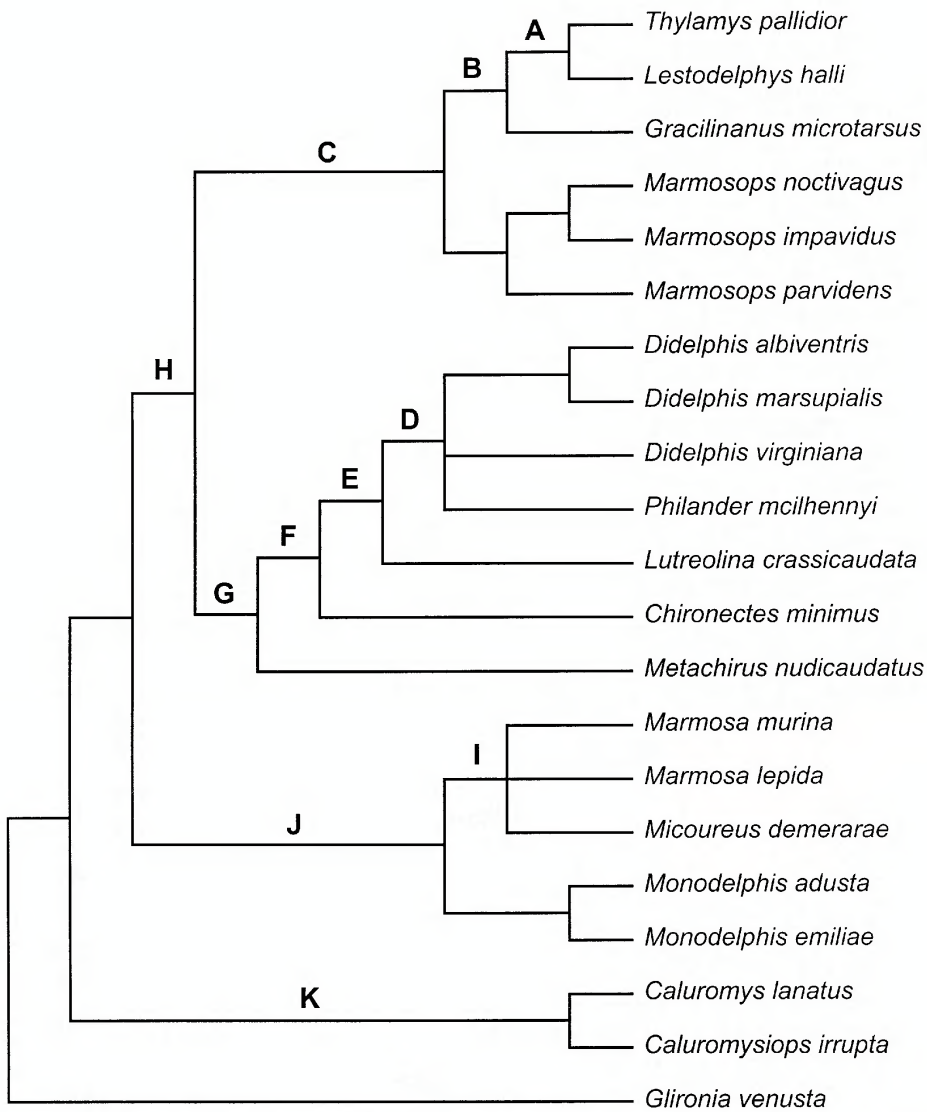

Fig. 1. Strict consensus of 18 equally most-parsimonious trees resulting from a heuristic analysis of IRBP sequences by Jansa and Voss (2000). For simplicity, placental outgroups and nondidelphid marsupial ingroup taxa (*Caenolestes*, *Dromiciops*, *Echymipera*, *Phascogale*, *Pseudochirops*, *Vombatus*) are not shown. Alphabetic labels (A, B, C, etc.) serve to identify clades for which formal taxon names are either unavailable or confusing due to conflicting usages.

MATERIALS AND METHODS

Taxon Sampling and Phylogenetic Assumptions

Herein we analyze nonmolecular character data and molecular sequences from all of the didelphids included in our first report (Jansa and Voss, 2000), together with *Caluromys philander* (part of our caluromyine outgroup, see below) and 14 additional didelphine species chosen (1) to increase taxon sampling density in regions of the tree previously identified as problematic, (2) to maximize diversity within previously undersampled polytypic genera, and (3) to optimize the nomenclatural relevance of our analytic results. In total, the 35 didelphids whose relationships are analyzed below represent about 44% of the currently recognized living species and all of the Recent genera that are unambiguously re-

ferable to the family (excluding *Hyladelphys*; see below).

In order to resolve the relationships of taxa currently referred to *Marmosa* and *Micoureus* we made a special effort to include representatives of every supraspecific unit of *Marmosa* (sensu stricto) recognized by the last monographer of this highly diverse genus (Tate, 1933). Whereas only *Marmosa murina* and *M. lepida* were analyzed as generic exemplars in our former study, our new dataset also includes *M. canescens* (a member of Tate's "*Canescens* Section"), *M. mexicana* (representing Tate's "*Mexicana* Section"), *M. robinsoni* (from Tate's "*Mitis* Section"), and *M. rubra* (classified with *M. murina* in Tate's "*Murina* Section"). We used biogeographic criteria and published analyses of mtDNA (Patton et al., 2000) to select maximally divergent exemplars of *Micoureus*, of which our dataset now includes two Amazonian species with highly divergent cytochrome-*b* sequences (*M. demerarae*, *M. regina*) and a nomenclaturally important taxon from the Atlantic Rainforest of southeastern Brazil (*M. paraguayanus*; see appendix 3).

To assess the reciprocal monophyly of *Philander* and *Didelphis*, we sought additional species of the former genus, which was previously represented in our dataset only by the western Amazonian form *P. mcilhennyi*. Our study now also includes *P. opossum* (the type species, from northeastern Amazonia; appendix 3) and *P. frenata* (from southeastern Brazil), of which the latter has the most divergent cytochrome-*b* sequences in the genus (Patton and da Silva, 1997; Patton et al., 2000).

Monodelphis, represented in our previous study by two western Amazonian species (*M. adusta* and *M. emiliae*), is a speciose genus whose phylogenetic diversity is now better sampled by including additional congeners. *Monodelphis theresa* (see appendix 3 for an explanation of our usage of this name) is an Atlantic Rainforest endemic that differs conspicuously from *M. adusta* and *M. emiliae* in external and basicranial characters, and *M. brevicaudata* is a nomenclaturally important northeastern Amazonian endemic (appendix 3) with a highly divergent cytochrome-*b* sequence (Patton and Costa, 2003). Our previous sampling of species-level diversity in two other speciose genera, *Marmosops* and *Thylamys*, is augmented by including one additional taxon from each (*M. incanus*, *T. venustus*). Lastly, one of the two terminals identified as *M. parvidens* in our earlier study is reidentified herein as *M. pinheiroi* based on subsequent revisionary work (Voss et al., 2001).

Because most of the significant problems remaining in didelphid phylogeny concern conflicting hypotheses of relationships within the subfamily Didelphinae, we designate that taxon as our ingroup, and we treat caluromyines as a composite outgroup in all of the analyses reported below. Although compelling support for didelphine monophyly is only provided by molecular data (Kirsch et al., 1997; Jansa and Voss, 2000), our use of multiple outgroup taxa provides a partial test of this assumption with nonmolecular characters. Ten uniquely derived and unreversed IRBP base substitutions supporting didelphid monophyly (Jansa and Voss, 2000: table IV) suggest that caluromyines are an appropriately close outgroup for this purpose.

The analyses reported below do not include *Hyladelphys*, a taxon that was provisionally referred to the family Didelphidae based on zoogeography and shared primitive characters (Voss et al., 2001). Instead, the ambiguous relationships of *Hyladelphys* require a larger analytic context that should include nondidelphid marsupials (e.g., dasyuromorphs and microbiotherians) and nonmarsupial metatherians (e.g., *Pucadelphys*; see Rougier et al., 1998) to effectively test relevant phylogenetic alternatives. Because morphological and molecular comparisons with such distant outgroups would substantially extend the scope of our study, we defer them to a subsequent report.

Taxonomic Identifications

All of the didelphid specimens from which morphological characters were scored and from which DNA was sequenced for this study (including those sequenced by Jansa and Voss, 2000) were identified by first-hand comparisons with types, original descriptions, or other relevant sources of taxonomic information. In some cases, the names we apply are not consistent with previously pub-

lished identifications of the same specimens, and we use some names that may be unfamiliar because they are not recognized as valid in standard taxonomic references (e.g., Wilson and Reeder, 1993). Relevant justifications for our taxonomic usages are explained in appendix 3.

Nonmolecular Character Survey and Coding Conventions

Our survey of didelphid nonmolecular characters is here restricted to external and craniodental morphology plus karyotypes. For most taxa we were able to examine multiple examples of each relevant specimen preparation type (skins, adult skulls, subadult skulls, juvenile skulls, fluid-preserved material; appendix 1). However, sample sizes were minimal or nil for some preparations of rare taxa (notably of the fluid-preserved parous females needed to score pouch and mammary characters). In such cases, we consulted published descriptions for second-hand observations. In the absence of any available information, we scored the relevant matrix cell as missing ("?"). We neither karyotyped any didelphid material ourselves, nor did we examine cell suspensions, slides, or other tangible products of karyotypic analysis. Instead, our scoring of chromosomal variation is based entirely on the literature.

Our initial survey of external and craniodental characters included every morphological feature reported to be taxonomically variable among didelphids in previous cladistic analyses of marsupial relationships (e.g., Kirsch and Archer, 1982; Creighton, 1984; Reig et al., 1987; Rougier et al., 1998; Wroe et al., 2000). Other potentially informative characters described in the comparative morphological literature (e.g., Bresslau, 1920; Lyne, 1959; Archer, 1976a, 1976b; Lunde and Schutt, 1999; Sánchez-Villagra and Wible, 2002) and in systematic monographs (e.g., Thomas, 1888; Osgood 1921; Tate, 1933, 1947; Hershkovitz, 1992b, 1997; Marshall and Muizon, 1995; Muizon, 1998) were also evaluated. Unfortunately, many of the characters we gleaned from the literature ultimately proved to be unsuitable for phylogenetic analysis for one or more of several reasons.

Characters reported to have distinctly different states in phylogenetic analyses or comparative surveys with just a few didelphid exemplars were often impossible to score unambiguously in our taxon-dense study due to the continuous variation introduced by anatomically intermediate forms. Other characters were found to be so consistently variable within species as to prevent confident scoring of rare taxa represented by small samples. Still other characters were judged to be redundant, either because of serial repetition (e.g., the occurrence of the same occlusal feature on successive teeth), functional reciprocity (e.g., correlated variation in occluding elements of the upper and lower dentition), or semantic equivalence (different ways of describing the same thing). Some characters were rejected because scoring them required uncommon specimen preparations (e.g., pouch young, serially sectioned skulls, isolated petrosals), the widespread absence of which would have resulted in more missing data than phylogenetically useful information. Several characters gleaned from the literature were difficult to interpret due to ambiguous state descriptors (e.g., "normal" versus "reduced") that could not be associated meaningfully with conditions observed in our material, and a few characters were found to be based on clearly erroneous observations. Relevant examples of such problems are discussed in the text or in footnotes, and an annotated list of rejected characters is provided in appendix 4.

Our dataset includes both parsimony-informative characters and autapomorphies. The latter were scored for several reasons. First, scoring autapomorphies is sometimes necessary to preserve homologies in unordered multistate characters that contain parsimony-informative states. Second, scoring autapomorphies is required for meaningful comparisons of morphological and molecular branch lengths (Omland, 1997). Third, including autapomorphies facilitates the recovery of taxon diagnoses from the data matrix, which would otherwise require supplementation for this purpose. Fourth, some traits that are autapomorphic among the taxa we examined could be parsimony-informative in a more taxon-dense analysis, so including them is useful for future applications of our dataset.

Although many didelphid morphological characters are binary, we constructed multistate characters in situations where three or more logically dependent alternative conditions were observed. In some cases, multistate characters could be ordered by the method of intermediates (Wilkinson, 1992), but in others no compelling justification for ordering could be found. Apparently, all coding conventions for inapplicable characters (e.g., morphology of the pouch in pouchless species) are unavoidably problematic (Maddison, 1993; Lee and Bryant, 1999; Strong and Lipscomb, 1999), but reductive coding seems to be the best option (Wilkinson, 1995). By this convention, the presence/absence and alternative conditions of a structure are scored as separate characters, with taxa lacking the structure in question scored as inapplicable for the character describing condition. Although we use a different symbol ("-") to indicate inapplicables in our data matrix, these were effectively analyzed as missing data ("?") due to the limitations of existing phylogenetic algorithms.

Whereas individual organisms are commonly treated as terminals in molecular phylogenetic studies (after Vrana and Wheeler, 1992), this is not a viable option for morphological datasets if some phylogenetically informative attributes are only expressed by adults, others by juveniles, some by males, and others by females. Because didelphid morphological characters include both age- and sex-dependent attributes, our terminals are necessarily composite entities, consisting of multiple individuals judged to be conspecific. Inevitably, examination of multiple conspecific specimens reveals that some species are polymorphic for some characters.

The phylogenetic analysis of intraspecific polymorphisms was recently reviewed by Wiens (2000), who recommended analyzing trait frequencies as numerical or interval data, but the coding complexities (a unique state for every taxon) and computations (involving large numbers of step matrices) required to implement frequency methods with real datasets are daunting. Unfortunately, most of the other methods discussed by Wiens (2000) seem indefensible because (1) they discard potentially useful phylogenetic information in the presence of rare variants (especially the "fixed only", "polymorphic", and "missing" options), (2) because they require a priori distinctions between primitive and derived conditions that are inappropriate when reversals are phylogenetically informative (the "any instance" option), or (3) because they introduce unnecessary homoplasy (the "unordered" option). The "unscaled" option favored by Campbell and Frost (1993), in which polymorphism is coded as a state intermediate to the fixed conditions with all state transformations assigned the same parsimony cost, has the unfortunate tendency to weight characters scored from common specimen preparations (e.g., adult dentitions, in which polymorphisms are more likely to be observed) more heavily than characters scored from uncommon preparations (e.g., fluid-preserved parous females), in which polymorphisms are seldom seen.

The traditional way to deal with rare variants in phylogenetic analyses of morphological data has been to ignore them by coding only the commonest (modal) condition for each species. This is defensible on the assumption that most matrix cells would be polymorphic if large enough samples of conspecific individuals were examined, so coding rare variants (humans with external tails, for example) as polymorphisms obscures useful phylogenetic information inherent in the most-frequent condition. Unfortunately, there is no biologically meaningful criterion for identifying rare variants as a distinct category of phenotypic traits that can be safely ignored by this method. Instead, nonmodal traits in conspecific samples range continuously from the genuinely rare to the almost-equally-common.

In fact, all methods for coding polymorphism appear to be suboptimal, resulting in problematic matrix entries or systematically biased results when applied uncritically. An alternative is to treat putative polymorphisms on a case-by-case basis, an approach that seems more realistic given the need to evaluate numerous alternative explanations for phenotypic variability (e.g., teratology, ontogeny, geographic variation) in real samples. In general, we scored the modal condition when this could be clearly recognized as such in our material. When no condition

was observed to be conspicuously more frequent than another, however, we coded polymorphisms using the "scaled" option (Wiens, 2000). By this convention, a character originally construed as binary (with two fixed conditions coded 0 and 1) would be recoded if a polymorphism were observed in one or more species. The recoded character would take the form of an ordered transformation series (0 ↔ 1 ↔ 2) with the intermediate state representing the polymorphism and the transformations 0 ↔ 1 and 1 ↔ 2 each having a weight of 0.5 relative to the unit weight (1.0) assigned to the transformation 0 ↔ 1 in a binary character without observed polymorphisms. As noted by Campbell and Frost (1993), this method implicitly assumes that all transformations from one fixed condition to another involve intraspecific polymorphisms whether or not these are actually observed.

In order to make our coding decisions as transparent as possible, we report our observations concerning intraspecific variability in the text following each character description. These accounts also serve to summarize relevant taxonomic patterns in our data, and to resolve any ambiguity in the necessarily terse state definitions provided. Discrepancies between our interpretation of morphological attributes and those of previous researchers who observed the same features are likewise stated and (if possible) explained. Throughout, our objective in writing each character account is to enable future workers to replicate our data and to apply the same criteria consistently for scoring taxa not included in this study.

Molecular Sequencing and Character Coding

For all specimens newly sequenced in this study (appendix 2), DNA was extracted from heart, liver, or kidney tissue that had been frozen or preserved in ethanol in the field. Procedures for DNA extraction and sequencing (including the names and locations of primers used in PCR reactions) were previously described by Jansa and Voss (2000). Briefly, a region approximately 1.2 kb long of IRBP exon 1 was amplified from genomic DNA using primers A and D1. This product was used as a template in two subsequent PCR reactions, one using primer A paired with F and one using primers E1 and D1. The resulting PCR product was sequenced in both directions using amplification primers and dye terminator chemistry (either BigDye or dRhodamine Ready Reaction Kits, Applied Biosystems Inc.). All sequences analyzed in this report have been deposited in GenBank with accession numbers AF257675–AF247710 (from Jansa and Voss, 2000) and AY233765–AY233791 (from this project).

Because IRBP nucleotide sequences do not vary in length among the taxa included in this study, alignments were constructed by eye with reference to translated amino acid sequences. In order to reduce computation time for phylogenetic analysis, we condensed redundant conspecific sequences to single terminals using the "filter taxa" option in MacClade 3.06. By this procedure, conspecific sequences were considered redundant if they were either identical or could be made identical by resolving missing or ambiguous character states.

We constructed two different molecular data matrices for phylogenetic analysis from this filtered collection of IRBP sequences. To construct the first matrix ("IRBP1"), we included all nonredundant sequences as terminal taxa, with the result that some species were represented by multiple terminals, while other species were represented by a single terminal—the same procedure used to compile the molecular data matrix analyzed in our first report (Jansa and Voss, 2000). For the purpose of combining molecular and nonmolecular data, however, we constructed a second matrix ("IRBP2") with species as terminal taxa; in this matrix, intraspecific polymorphisms created by condensing conspecific sequences to single terminals were scored with appropriate IUPAC ambiguity codes. Because only a few species are represented by two or more nonidentical sequences in this study, modal states could seldom be identified as such, and no account was therefore taken of base frequencies when scoring polymorphisms (e.g., A-or-G was coded as R even if G was observed in two out of three conspecific individuals). We did not used the "scaled" option discussed above for nonmolecular character polymor-

phisms because the resulting step matrices would have greatly increased the computational task of analyzing these data.

Parsimony Methods

Each of the three datasets described above (nonmolecular, IRBP1, IRBP2) as well as the supermatrix obtained by combining the nonmolecular data with IRBP2 were analyzed using heuristic parsimony searches implemented by PAUP* 4.0b10 (Swofford, 1998). Whereas some multistate nonmolecular characters were analyzed as ordered transformation series, IRBP sequence characters were always treated as unordered. All characters (nonmolecular and IRBP) were equally weighted in all analyses. Each heuristic parsimony search employed 1000 replicates of random taxon addition with TBR branch swapping. Bremer support (Bremer, 1994) for each resolved node in the strict consensus of equally most-parsimonious trees was calculated using TreeRot version 2a (Sorenson, 1999) to create the appropriate constraint files and PAUP* commands. Bootstrap values (Felsenstein, 1985) were calculated from heuristic parsimony analyses (each with 10 random-addition replicates, TBR branch swapping, and 5 saved trees) based on 1000 pseudodoreplicated data matrices.

In order to evaluate previous concepts of taxonomic membership within a parsimony framework, we interpreted nominal taxa (e.g., *Marmosa* sensu Tate, 1933) as hypotheses of monophyly and ran heuristic searches (with 100 random-addition sequences and TBR branch swapping) for the most parsimonious tree consistent with such constraints. The parsimony cost implied by a given concept of taxonomic membership was then computed as the length of the most-parsimonious tree on which the taxon in question is monophyletic minus the length of the most-parsimonious unconstrained tree.

Likelihood Methods

In order to explore the phylogenetic consequences of adopting an explicit model of IRBP sequence evolution, we tested several models and used the one that best fit our data to evaluate alternative trees by the maximum-likelihood criterion (see Steel and Penny [2000] for a recent review of such methods and a discussion of their links to maximum parsimony). In order to reduce the computation time necessary for a thorough tree search, we performed all likelihood analyses on the condensed-taxon dataset (IRBP2). We first computed a neighbor-joining tree based on Jukes-Cantor corrected distances (Jukes and Cantor, 1969), and we used that topology to calculate log-likelihood scores and to estimate relevant parameter values under eight models of nucleotide substitution: Jukes and Cantor (1969; JC69), Felsenstein (1981; F81), Hasegawa et al. (1985; HKY), Tamura and Nei (1993; TrN), Kimura (1980; K2P), Kimura (1981; K3P), Zharkikh (1994; SYM), and Rodriguez et al. (1990; GTR). We also assessed whether including parameters for site-specific rate heterogeneity (the Γ-distributed rate parameter; Yang, 1994) and for a proportion of invariant sites (I) improved the fit of the model to the data. Lastly, we evaluated whether enforcing a molecular clock provided a better fit to the data than allowing substitution rates to vary from branch to branch across the tree. We accepted as the best-fit model that one for which additional parameters no longer significantly improved the log-likelihood score, as determined by likelihood-ratio tests (Goldman, 1993; Huelsenbeck and Rannala, 1997). For such tests, twice the difference in log-likelihood scores ($-2 \ln \Lambda = 2[\ln L_1 - \ln L_0]$, where $\ln L_1$ is the likelihood of the more parameter-rich model) was evaluated for statistical significance against a χ^2 distribution with degrees of freedom equal to the difference in the number of parameters between the two models minus one. Subsequent to model evaluation and selection, the maximum-likelihood tree for IRBP2 was determined using a heuristic search (with ten random-addition replicates and TBR branch-swapping) in which the parameter values estimated by the best-fit model were used to calculate log-likelihood scores for each topology. Bootstrap analysis was performed under the best-fit likelihood model using 100 replicates of the "fast" stepwise addition procedure in PAUP*.

Combined Analysis

Although the desirability of obtaining character data from a diversity of phenotypic

and genomic sources is universally acknowledged, the circumstances under which different datasets can be validly combined for phylogenetic analysis are widely debated (de Queiroz et al., 1995). In the event that two datasets analyzed separately support significantly incongruent phylogenetic hypotheses, some authors (e.g., Bull et al., 1993) have argued that a combined analysis is unjustified, but no effective method for mediating dataset conflicts has been proposed for such cases. Potential advantages of combined-data analysis (whether or not separate analyses produce incongruent results) include increased phylogenetic resolution (because different datasets are sometimes informative at different taxonomic levels; e.g., Pennington, 1996), the discovery of robust clades not (or only weakly) supported by separate analyses (e.g., Gatesy et al., 1999b; Gatesy and Arctander, 2000), and the avoidance of arbitrariness in recognizing data partitions (Baker and DeSalle, 1997; Siddall, 1997; Wetterer et al., 2000).

We combined our nonmolecular and IRBP sequence data and analyzed the resulting supermatrix using parsimony as described above. We did not use the Incongruence Length Difference test (Farris et al., 1995a, 1995b) to evaluate dataset incongruence due to its inflated type 1 error rate and other statistical shortcomings (Barker and Lutzoni, 2002). Due to the large number of equally most-parsimonious trees resulting from our combined-data analysis, we did not calculate partitioned Bremer support values (another tool for quantifying dataset incongruence; Baker and DeSalle, 1997), which can be misleading when averaged in such situations (Lambkin et al., 2002). Instead, patterns of congruence and incongruence in our separate results were evaluated by direct inspection of trees and their associated measures of nodal support.

Online Data Archives

All three data matrices described above (nonmolecular, IRBP1, IRBP2) together with the combined-data supermatrix (nonmolecular + IRBP2) can be downloaded from ftp://ftp.amnh.org/pub/mammalogy.

NONMOLECULAR CHARACTERS AND ANALYTIC RESULTS

For convenient reference, our nonmolecular character descriptions are organized under headings that correspond to conventionally recognized sources of taxonomic variation (external morphology, cranium and mandible, dentition, and karyotypes). With the exception of karyotypes, we do not regard these categories as biologically meaningful partitions of the didelphid phenotype. Rather, each is associated with different traditions of scholarship and terminology that merit introductory comments, and problems of observation or interpretation affecting some categories require brief explanation. The main purpose of these accounts, however, is to explain the correspondence between numerical data codes and the a priori hypotheses of morphological or chromosomal homology upon which subsequent phylogenetic analyses depend.

External Morphology

Although tail prehensility, mammary formulae, the presence or absence of a pouch, and other external features have occasionally been coded for phylogenetic analysis in previous studies of marsupial relationships, the paleontological focus of most studies has resulted in datasets that are much richer in osteological than integumental characters. Indeed, entire classes of external characters have been ignored as sources of phylogenetic information. Patterns of integumental pigmentation, for example, are commonly described in the alpha-taxonomic literature (e.g., by Thomas, 1888; Tate, 1933; Hershkovitz, 1992b, 1997), but none has been coded for analysis in previous studies of didelphid relationships. Such inattention is hard to justify because some pelage markings exhibit less intraspecific variation and are easier to score as discrete states than are many routinely analyzed craniodental attributes. The following character descriptions are organized in a rostral-to-caudal sequence and include all phylogenetically informative traits that are more easily scored by external examination than by dissection or skeletal preparation, regardless of whether or not they are properly considered integumental. Thus, tax-

onomic differences in digital proportions are described below despite their obviously osteological basis. Except as noted otherwise below, our terminology for external morphological features follows usages defined or referenced by Brown (1971) and Brown and Yalden (1973).

Character 1: *Rhinarium with two ventrolateral grooves flanking the median sulcus on each side (0); or with a single ventrolateral groove on each side (1).* The didelphid rhinarium is divided by a median crease or sulcus (sulcus medianus; Ade, 1999) that extends from between the nares to the margin of the upper lip. On either side of this dividing fold, the ventral margin of the rhinarium is notched by one or two distinct grooves (fig. 2). Two ventrolateral grooves are present on each side in all examined caluromyines and most "marmosines", but only a single groove was observed in *Chironectes*, *Didelphis*, *Lestodelphys* (P. Jenkins, personal commun.), *Lutreolina*, *Metachirus*, *Monodelphis*, *Philander*, and *Thylamys pallidior*. We scored *Marmosa rubra* as missing ("?") in the absence of suitably preserved material. First noted by Thomas (1888), this character appears to have been ignored by subsequent students of didelphid systematics.[2]

Character 2: *Dark midrostral stripe absent (0); or present (1).* A median streak of dark fur, unconnected with any other dark marking, extends from the rostrum to the frontal region (between the eyes) in both examined species of *Caluromys* (fig. 3, top right). In other didelphids, a chevron of dark coronal fur sometimes extends anteriorly between the ears and down the rostral midline, but the condition seen in *Caluromys* is distinctive and apparently nonhomologous.

Character 3: *Fur surrounding eye not distinctively colored (0); or eye surrounded by mask of dark fur (1).* The circumocular fur is not distinctively colored in *Caluromysiops*, *Lutreolina*, or *Monodelphis*, but most other didelphids have mask-like markings (fig. 3). A circumocular mask or ring of dark (usually blackish) fur that contrasts sharply with the paler (usually brownish, whitish, or grayish) color of the crown and cheeks is present in "marmosines", *Glironia*, and *Lestodelphys*. Species of *Caluromys* have essentially similar reddish-brown eye rings that contrast with grayish cheeks and crowns. A blackish mask is likewise present in all examined species of *Didelphis*, but this marking is inconspicuous in *D. marsupialis* and *D. virginiana*. We also scored a mask as present (state 1) in *Metachirus*, *Chironectes*, and *Philander*, taxa whose dark circumocular fur is continuous with dark fur on the crown of the head.

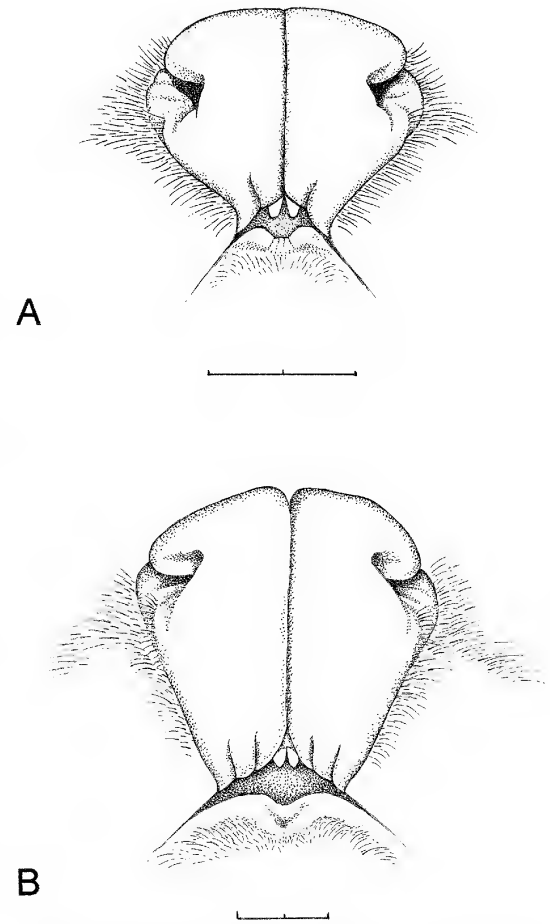

Fig. 2. Ventral view of rhinarium in *Thylamys pallidior* (**A,** UMMZ 156349) and *Marmosa robinsoni* (**B,** UMMZ 117236). Only a single groove is present on the ventral margin of the rhinarium to either side of the median sulcus in *T. pallidior*, whereas two ventrolateral grooves are present in *M. robinsoni*. Scale bars = 2 mm.

[2] Ade (1999: plate VII, fig. E) illustrated the ventrolateral rhinarial grooves of *Monodelphis domestica* but did not name them or remark any taxonomic variation in this trait, which is not present in any of the eutherians described in his useful review of rhinarial morphology.

Fig. 3. Facial markings of didelphid marsupials scored for characters 2–5. **Top left,** *Marmosa robinsoni* (dark midrostral stripe absent; circumocular mask present, contrasting with coloration of cheeks and crown; pale spot above each eye absent), score: 0100. **Top right,** *Caluromys lanatus* (dark midrostral stripe present; circumocular mask present, contrasting with coloration of cheeks and crown; pale spot above each eye absent), score: 1100. **Bottom left,** *Lutreolina crassicaudata* (dark midrostral stripe absent; circumocular mask absent; pale spot above each eye absent), score: 00–0. **Bottom right,** *Philander opossum* (dark midrostral stripe absent; circumocular mask present, continuous with dark coronal fur; pale spot above each eye present), score: 0111. Photographs by Pascual Soriano (top left, top right, bottom left) and Nancy B. Simmons (bottom right).

Character 4: *Circumocular mask contrasts with coloration of cheeks and crown (0); or polymorphic (1); or dark fur around eye continuous with dark coronal fur (2).* When present, the didelphid circumocular mask is either discrete (contrasting abruptly in coloration with the surrounding genal and coronal fur; fig. 3, top left), or it is continu-

ous with dark fur that covers the crown (between the ears; fig. 3, bottom right). In *Philander frenata*, however, both conditions occur with equal frequency in the material we examined. This character was scored as inapplicable ("-") for taxa that lack a mask of distinctively colored circumocular fur (see character 3, above).

Character 5: *Conspicuous pale spot above each eye absent (0); or present (1).* A distinct whitish supraocular spot is consistently present in species of *Metachirus* and *Philander*, resulting in the "four-eyed" marking by which these animals are commonly known (fig. 3, bottom right). Most other didelphids lack pale supraocular markings. An indistinct pale bar above each eye in *Chironectes* appears to be part of the unique transverse banding pattern in that taxon (see Character 7), rather than a homolog of the condition seen in *Metachirus* and *Philander*.

Character 6: *Gular gland absent (0); or present (1).* As described by Tate (1933: 30), many didelphids have a cutaneous gular (throat) gland, the presence of which is indicated on dried skins and fluid-preserved specimens by a bare median patch of skin; often, but not invariably, the surrounding fur is discolored. According to Barnes (1977: 390), this secretory region contains "hypertrophied apocrine sudoriferous glands and sebaceous glands, both confined to the thickened dermis". Because external signs of glandular activity tend to be maximally developed in fully mature males (op. cit.), we only scored this character if suitable adult male material (skins or fluid-preserved specimens) was examined.

No unambiguously glandular throat patch was observed in any examined specimens of *Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis virginiana*, *Lutreolina*, *Marmosa canescens*, *M. lepida*, *M. murina*, *M. rubra*, *Marmosops impavidus*, *M. parvidens*, *M. pinheiroi*, *Micoureus*, *Monodelphis theresa*, or *Philander*. Although most examined adult males of *Didelphis albiventris* and *D. marsupialis* had discolored gular fur, no glandular skin was macroscopically distinguishable in these taxa, for which we scored throat glands as absent. Because no adult male specimens of *Glironia* were examined, we scored this taxon as missing ("?") in our matrix. Adult males of all other taxa exhibited well-developed gular glands. Tate (1933: 30) reported that throat glands are absent in *Marmosops incanus*, but every adult male skin and fluid-preserved specimen of *M. incanus* that we examined (e.g., MVZ 182768, 182769) had conspicuous gular patches of obviously glandular skin.

Character 7: *Dorsal body pelage more-or-less uniformly colored, unpatterned (0); or marked by dark transverse bars (1); or marked by paired scapular stripes (2); or marked by one median and two lateral stripes (3); or grayish middorsum contrasting with reddish or yellowish flanks (4); or grayish midbody (including flanks) contrasting with reddish head and rump (5); or "tricolored" (6).* The dorsal body pelage of most didelphids is uniformly colored and essentially unpatterned (state 0), although some taxa assigned to this state are indistinctly darker middorsally than along their paler flanks. States 1–5 are autapomorphies for this study, but we scored them for descriptive completeness and to accommodate denser taxon sampling in future datasets. Among taxa scored in our current matix, dark transverse bars (state 1) are unique to *Chironectes*; dark scapular stripes (state 2) are unique to *Caluromysiops*; three longitudinal stripes (state 3) are unique to *Monodelphis theresa*; a grayish middorsum contrasting with reddish flanks (state 4) is unique to *Monodelphis brevicaudata*; and a grayish midbody contrasting with reddish head and rump (state 5) is unique to *Monodelphis emiliae*. The subtle but consistently diagnostic "tricolor" shading of *Thylamys* and *Lestodelphys* (state 6) was described by Tate (1933: 209) as follows:

> Instead of the usual bicolor system composed of a dorsal color, paling a little on the sides, which is replaced at a generally well-marked transition line by a distinct ventral color, the *elegans* group [= *Thylamys*] displays three distinct shades, separated from each other along each side by two lines of transition. The additional lines are subdorsal, running from a point at the center of the frons [forehead] past the inner edge of each ear (not including it), and straight backward through scapulae and hips, where they again approach the median line of the body and merge with the tail. This pair of lines encloses the major part of the dorsal area of head and body, the color of the area being very dark brownish-gray or grayish fuscous.

> The fuscous area is pointed at front, projecting forward between the ears, and narrows again to a point as it merges with the dark color of the upper surface of the tail. The second [lateral] area, light gray in color, frequently tinged with buffy or yellowish, extends [on each side] between the dark dorsal region and the edge of the belly color at the normal transition line. Ventral color either buffy, grayish, or snowy white.

Color illustrations of most of these dorsal pelage patterns are in Eisenberg (1989), Redford and Eisenberg (1992), Pérez-Hernández et al. (1994), Reid (1997), and Eisenberg and Redford (1999). In the absence of any obvious sequence of transformations among alternative dorsal fur markings, this character was treated as unordered in all of our analyses.

Character 8: *Dorsal underfur dark (0); or white (1).* The hair bases of the dorsal fur are pigmented, usually dark gray (or grayish), in most didelphids. Species of *Didelphis*, however, uniquely exhibit white underfur.

Character 9: *Dorsal pelage hairs not grossly dissimilar in length or coarseness (0); or dorsal pelage with guard hairs conspicuously longer and coarser than underfur (1).* Very long coarse guard hairs that project conspicuously from the underfur are uniquely exhibited by species of *Didelphis*. Patton and da Silva (1997) characterized the guard hairs of *Philander mcilhennyi* as diagnostically longer than those of other congeners, but specimens of *P. mcilhennyi* that we examined do not approach the condition coded above as state 1.

Character 10: *Manual digit III longer than other manual digits (0); or manual digits III and IV subequal and longer than other manual digits (1); or manual digit IV longer than other manual digits (2).* According to Tate (1947: 108), the third and fourth digits of the didelphid manus are subequal and longer than the other manual digits, proportions that correspond to the paraxonic morphotype defined by Brown and Yalden (1973). Not all didelphids have paraxonic forefeet, however. Instead, many have a mesaxonic manus in which dIII is distinctly longer than the other fingers; taxa that we scored as exhibiting this condition include *Chironectes*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Marmosops*, *Metachirus*, *Monodelphis*, *Philander*, and *Thylamys*. A third alternative condition is seen in *Caluromys* and *Caluromysiops*, in which manual digit IV is distinctly longer than dIII. On the hypothesis that these three conditions represent a sequence of transformations reflecting the dominance of either III or IV as the main propulsive digit of the didelphid manus (with the subequal condition intermediate to the other two states), we treated this character as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) in all of our analyses.

Because the hardened digits of dried skins are often twisted, folded, or otherwise distorted, this character (and character 14, below) is more confidently scored from fluid-preserved material with elastic phalangeal joints that can be manipulated to align adjacent digits for relative length comparisons.

Character 11: *Central palmar surface of manus smooth, or sparsely provided with large flattened tubercles (0); or densely covered with small convex tubercles (1); or entire plantar surface of manus sandpapery, covered with microscopically dentate tubercles (2).* The central palmar epithelium (the region of bare skin encircled by the plantar pads) of the manus is smooth in most didelphids, but the palms are very densely set with small convex tubercles in *Thylamys* and *Lestodelphys*. A few didelphids (e.g., *Marmosa canescens*, *Monodelphis theresa*) have manual palms that are sparsely provided with large flattened or weakly convex tubercles, a condition that more nearly resembles the common didelphid condition than that seen in *Thylamys* and *Lestodelphys*. Sandpapery plantar epithelium is an autapomorphy of *Chironectes* (see Hamrick, 2001) that cannot be confidently associated with either of the other states of this unordered character. Creighton (1984: characters 2, 6) scored the palmar texture of manus and pes as separate characters, but the taxonomic distribution of the states he recorded suggests that they do not result from independent transformations.

Character 12: *Externally conspicuous lateral carpal tubercles absent in both sexes (0); or large adult males with a prominent lateral carpal tubercle supported internally by the pisiform (1).* In most didelphids the wrists of males and females are morphologically similar, but striking sexual dimorphism is present in some "marmosines" (Lunde and Schutt, 1999). Grossly enlarged glabrous

tubercles supported internally by carpal ossifications are exhibited by large adult males of *Gracilinanus*, *Marmosops*, *Micoureus*, and some species of *Marmosa*. Two distinct kinds of tubercles can be distinguished, consisting of lateral ("ulnar") tubercles supported internally by the pisiform, and medial ("radial") tubercles supported by the prepollex (op. cit.). Although some intraspecific variation in the development of carpal tubercles has been documented, most examples can be attributed to ontogeny: tubercles are consistently present in the largest adult male specimens of species in which such structures occur, even though they may be lacking in some smaller (presumably younger) conspecific males.

Lateral carpal tubercles supported internally by the pisiform (Lunde and Schutt, 1999: fig. 2) are more widespread than medial carpal tubercles, occurring in all examined taxa that exhibit any conspicuous sexual dimorphism in the wrist. We scored these structures as present in adult males of *Marmosa canescens*, *M. lepida*, *M. mexicana*, *M. robinsoni*, *M. rubra*, *Marmosops*, and *Micoureus*. We scored *Glironia* and *Gracilinanus microtarsus* as missing ("?") for this character in the absence of suitably preserved material. All other examined didelphid taxa appear to lack lateral carpal tubercles. Our observations differ from those of Lunde and Schutt (1999: table 1), who scored lateral ("ulnar") tubercles as absent in *Marmosa mexicana*, *M. robinsoni*, *M. rubra*, and *Micoureus demerarae*. In fact, the hypertrophied pisiform seems to be more closely applied to the center of the wrist (and therefore somewhat less prominent) in *Marmosa* and *Micoureus* than it is in *Marmosops*, but we defer scoring such positional distinctions pending examination of relevant osteological preparations from all of the taxa in our study.

Character 13: *Externally conspicuous medial carpal tubercles absent in both sexes (0); or large adult males with a prominent medial tubercle supported internally by the prepollex (1).* We observed medial carpal tubercles (Lunde and Schutt, 1999: fig. 3) in large adult male specimens of *Marmosa mexicana*, *M. robinsoni*, *M. rubra*, and *Micoureus*. Because no suitably preserved material of *Glironia* and *Gracilinanus microtarsus* was available for examination, we scored these taxa as missing ("?"). Medial carpal tubercles appear to be consistently absent in all of the other didelphid taxa examined.

Character 14: *Pedal digit III distinctly longer than adjacent digits II and IV (0); or pedal digits II–IV subequal (1); or pedal digits II–IV progressively increasing in length, with IV distinctly longer than III (2).* In *Lestodelphys*, *Lutreolina*, and *Monodelphis* the third pedal digit is longer than the adjacent second and fourth digits, and the hind foot is therefore mesaxonic (sensu Brown and Yalden, 1973) despite the opposability of digit I. By contrast, pedal digits II, III, and IV are subequal (none distinctly longer than the others) in *Didelphis albiventris* and *D. virginiana*. Among all other examined didelphid taxa (including *Didelphis marsupialis*), the second, third, and fourth pedal digits progressively increase in length, such that dIV is the longest toe opposing the hallux (see Boas, 1918: figs. 2, 3). Although taxonomic variation in pedal digit lengths was previously scored for phylogenetic analysis by Creighton (1984: character 9), his observations for *Lestodelphys* (said to have a long fourth digit) and *Lutreolina* (said to have subequal third and fourth digits) differ inexplicably from ours. Note that the states of this character do not covary with those of character 10, as might be expected if transformations of manual and pedal morphology were functionally or developmentally determined by the same factors. For example, whereas dIII is the longest manual digit in *Marmosops*, dIV is the longest pedal digit in that genus.

Character 15: *Pedal digits free, without extensive webbing (0); or all pedal digits bound together by extensive fleshy webs (1).* Webbed hind feet (illustrated by Augustiny, 1942: fig. 17; Mondolfi and Medina, 1957: fig. 3; Oliver, 1976: fig 1C; and Hershkovitz, 1997: fig. 3) are a conspicuous autapomorphy of *Chironectes*.

Character 16: *Plantar epithelium of tarsus entirely or partly glabrous (0); or densely covered with coarse fur (1).* In most didelphids the plantar surface of the hindfoot appears to be glabrous (hairless) from toetips to heel. In others (e.g., *Marmosops*) the distal tarsus is partially covered by a velvet-

like pelage of microscopic hairs, but there is still a glabrous patch of skin at the apex of the heel. Because a range of intermediates blur the distinction between these two conditions (as when a narrow band of glabrous epithelium connects the naked apex of the heel to the broader expanse of naked skin over the metatarsus), we combine them as a single state (0). By contrast, the tarsus is entirely covered by coarse (macroscopic) hairs in *Lestodelphys* and *Thylamys*, an unambiguously different morphology that we code accordingly (as state 1).

Character 17: *Pouch absent (0); or present (1).* Based on our examination of parous adult female specimens, pouch-like enclosures for nursing young are unequivocally present or absent among the didelphid taxa included in this study. Although our sample sizes were always small, we observed no intraspecific variation in this character, nor did we observe any intermediate condition between absence and presence of a pouch. Despite the fact that distinctly different pouch configurations (scored as a separate character, below) can be recognized within the family, we provisionally recognize all such enclosures as homologous in the absence of a priori evidence to the contrary.

We found no trace of a pouch in suitable material (fluid-preserved specimens and carefully prepared skins) of parous adult female *Glironia*, *Gracilinanus*, *Lestodelphys*, *Marmosa*, *Marmosops*, *Metachirus*, *Micoureus*, and *Monodelphis*. Well-developed pouches were consistently found to be present in suitably prepared parous adult female *Caluromys*, *Chironectes*, *Didelphis*, and *Philander*. Although *Lutreolina* was described as pouchless by Thomas (1888), Cabrera (1919), and Marshall (1978a), two fluid-preserved specimens that we examined (UMMZ 166634, USNM 536827) had pouches exactly resembling the morphology illustrated and described by Krieg (1924: fig. 11).[3] We scored *Caluromysiops* as having a pouch based on statements to that effect by Izor and Pine (1987) and Reig et al. (1987), but the absence of compelling documentation (explicit descriptions or illustrations of examined specimens) is noteworthy, and our scoring should be considered provisional. Lacking suitable specimens or reliable literature descriptions of parous adult female specimens, we scored *Monodelphis theresa*, *Thylamys pallidior*, and *T. venustus* as missing ("?") for this character.

Some noteworthy confusion exists concerning the presence or absence of a pouch in *Metachirus*. Despite the fact that this genus was clearly described and illustrated as having a well-developed pouch by Enders (1937), all previous and subsequent authors have described it as pouchless, and none of the parous adult females we examined (AMNH 255815; USNM 461138, 577756) had any trace of a marsupium. Enders himself (in a personal communication cited by Pine, 1973) believed that he was mistaken in his taxonomic identification of pouched specimens that he earlier reported as *Metachirus*, which were unfortunately not preserved as vouchers. Given these reasons to doubt the reliability of Enders' (1937) observations, we scored *Metachirus* as pouchless rather than polymorphic.

Character 18: *Pouch consists of separate lateral skin folds opening medially (0); or lateral folds connected posteriorly, pouch opening anteriorly (1); or lateral folds connected anteriorly, pouch opening posteriorly (2).* The marsupium of *Caluromys philander* uniquely consists of deep lateral skin folds that enclose the nursing young and open in the midline (resembling the morphology that Tyndale-Biscoe and Renfree [1987: fig. 2.8] incorrectly attributed to didelphids in general). In *Caluromys lanatus*, *Didelphis*, and *Philander*, however, the lateral pockets are joined posteriorly, forming a more extensive enclosure that opens anteriorly (Enders, 1937: fig. 19). Yet another condition is exhibited by *Chironectes* and *Lutreolina*, in which the lateral pockets are connected anteriorly, forming a marsupium that opens posteriorly (Krieg, 1924: fig. 11A; Oliver, 1976: fig. 1B). We scored this character as inapplicable ("-") for all pouchless species, but we scored *Caluromysiops* (whose pouch morphology has not been described) and the few taxa for which it is not certain whether a pouch is present or absent as missing

[3] Reig et al. (1987) reported another pouched museum specimen of *Lutreolina*, but they did not code this taxon for presence or absence of a pouch in their data matrix.

("?"). In the absence of any clear indication of intermediacy among the alternative conditions of the didelphid marsupium, this character was treated as unordered in all of our analyses.

Character 19: *Mammae all abdominal/inguinal, more-or-less confined to pouch region (0); or extending anteriorly beyond pouch region to thoracic region (1).* In all marsupials that possess a pouch the mammae are contained within it, but the mammae of pouchless taxa are variously distributed (see Tate, 1933: fig. 3). In most pouchless didelphids (e.g., *Glironia*, *Marmosa*, *Micoureus*, *Metachirus*, some species of *Marmosops*, and some species of *Monodelphis*), the mammae are confined to a more-or-less circular inguinal/abdominal array that occupies the same anatomical position as the pouch does in taxa that possess a marsupium. In other pouchless didelphids (e.g., *Lestodelphys* and *Marmosops incanus*), however, bilaterally paired mammae extend anteriorly well beyond the pouch region. Although most of these anterior teats are not actually located on the upper chest, they are usually referred to as "pectoral" mammae by authors (e.g., Tate, 1933; Reig et al., 1987: character 42). Because the presence or absence of pectoral mammae cannot be confidently inferred from published teat counts (e.g., those tabulated by Bresslau, 1920), and because unused mammae are inconspicuous, examination of well-preserved parous adult females is essential for accurate scoring of this character. We were unable to examine suitable material of *Gracilinanus microtarsus* ourselves, but we scored pectoral mammae as present in this taxon based on Tate's (1933: 193) description and illustration (op. cit.: fig. 3) of a fluid specimen formerly preserved in the British Museum of Natural History (BMNH 82.9.30.42).[4] We scored *Caluromysiops irrupta* as having only inguinal/abdominal mammae based on the reported presence of a pouch in that taxon (see character 17, above). Tate (1933) and Reig et al. (1987) reported pectoral mammae as present in *Monodelphis*, but the *Monodelphis* specimens we examined had only abdominal/inguinal teats. Lacking suitable material, we scored *Micoureus paraguayanus*, *Monodelphis theresa*, *Thylamys pallidior*, and *T. venustus* as missing ("?") for this character.

Character 20: *Urogenital and rectal openings closely juxtaposed and sharing a common mucosa (0); or urogenital and rectal openings widely separated by furred skin (1).* In most didelphids the openings of the urogenital and rectal ducts are closely juxtaposed and share a continuous mucosa. In life, both openings are normally recessed in a common sinus (cloaca), but this feature is obscured in male specimens with everted genitalia. *Chironectes* uniquely lacks a cloaca because the urogenital and rectal openings are widely separated by furred skin (Oliver [1976: fig. 1] correctly illustrated this morphology in the female, but his illustration of the male omits the urogenital orifice). Scoring this character requires fluid-preserved specimens, which were unavailable for *Marmosa rubra* (scored as missing ["?"] in our matrix). In a few cases, relevant published information was used to score taxa that we were unable to examine (e.g., Nogueira et al.'s [1999a] description of *Glironia*), but the literature also contains misleading information about didelphid cloacal anatomy.

Hershkovitz (1992a: 203–205; 1992b: 11–13) reported a diversity of cloacal types among marsupials, including: (1) consistent lack of separation between the urogenital and rectal openings (cloaca present in both sexes); (2) male urogenital and rectal openings separated by a "perineal membrane" or "perineum" (cloaca absent in males, present in females); and (3) consistent separation of urogenital and rectal openings (cloaca absent in both sexes). He explicitly attributed the first condition to *Caluromys*, *Gracilinanus*, and some species of *Marmosa*; the second to *Caluromysiops*, *Marmosops*, *Metachirus*, and *Micoureus*; and the third to the large $2n = 22$ opossums ("didelphids" in his usage).

Our side-by-side comparisons of specimens of taxa representing each of Hershkovitz's morphotypes revealed no corresponding differences in their cloacal anatomy with the unique exception of *Chironectes* noted above. For example, adult male specimens of

[4] Only the extracted skull of this specimen could be located during a recent search of the BMNH collections (P. Jenkins, personal commun.).

Caluromys lanatus (supposedly representing cloacal type 1; e.g., AMNH 273038) and *Caluromysiops irrupta* (type 2; e.g., FMNH 60398) exhibit identical arrangements of the urogenital and rectal openings. Likewise, Nogueira et al.'s (1999b) detailed study of male reproductive anatomy did not reveal any differences in the cloacal anatomy of *Caluromys* (allegedly type 1), *Metachirus* (type 2), and *Didelphis* (type 3). The only plausible explanation for Hershkovitz's unrepeatable and clearly problematic observations is that they resulted from careless interpretation of preservational artifacts.[5]

Character 21: *Body pelage extends onto tail conspicuously farther dorsally than ventrally (0); or body pelage extends onto dorsal and ventral surfaces of tail to about the same extent (1); or body pelage does not extend appreciably onto tail (2).* Body pelage, here defined as soft fur composed of ordinary coat hairs that are not associated with epidermal scales, extends to a variable extent onto didelphid tails. Body fur extends onto the tail much farther dorsally than ventrally in *Caluromys lanatus*, *Caluromysiops*, *Glironia*, *Monodelphis brevicauda*, and *M. emiliae*. By contrast, body fur extends onto the tail dorsally and ventrally to about the same extent (from about one-sixth to about one-third the length of that organ) in *Caluromys philander*, *Chironectes*, *Didelphis*, *Lutreolina*, *Micoureus paraguayanus*, and *Philander*. In the remaining taxa examined for this study (*Gracilinanus*, *Lestodelphys*, *Marmosa*, *Marmosops*, *Metachirus*, *Micoureus demerarae*, *M. regina*, *Monodelphis adusta*, *M. theresa*, *Thylamys*) body fur does not extend more than a short distance onto the tail base (less than or equal to about one-eighth of caudal length). In the absence of any obvious intermediates among these alternative conditions, we treated this character as unordered in all of our analyses.

Character 22: *Caudal integument uniformly pigmented or indistinctly or irregularly marked (0); or blackish basally and abruptly whitish distally (1).* Pale tail tips are not uncommon among didelphids, but the observed range of taxonomic variation exhibits few discontinuities for character-state definition. The exposed skin of most didelphid tails is grayish or brownish and, in most taxa with pale tail-tips, the color transition is either gradual (the basal color fading to white) or irregular (mottled). Dorsoventrally bicolored tails (which are grayish or brownish above and pale on the underside) represent another caudal marking pattern that is difficult to score as a discrete character state because it is indistinct in some taxa.

By contrast, the tails of *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* are blackish basally with abruptly white tips. Hershkovitz (1997: 34) confusingly described the tail of *Philander* as "entirely brown or mottled to particolored from tip to as much as distal three-fifths of tail more or less unpigmented", but all of the specimens of *Philander* that we examined (with the exception of obviously discolored material) have clearly black-and-white tails. This marking is variable in *Lutreolina* (a few specimens having all-black tails), but most (75%) of the skins we examined have white-tipped tails, and we scored this modal condition rather than create an intermediate state for intraspecific polymorphism. In *Chironectes*, 38 of 40 examined specimens (95%) had black tails with white tips. Although significant geographic variation has been reported in the extent of the white caudal marking within some *Didelphis* species (Gardner, 1973: 10–11), the pattern itself seems remarkably persistent—no population having been described with all-black or all-white tails—and we did not observe any intraspecific polymorphism in our samples of this genus.

Character 23: *Tail scales in predominantly annular series (0); or in annular and spiral series (1); or in predominantly spiral series (2).* The epidermal scales that cover the unfurred nonprehensile surfaces of didel-

[5] Other remarks about reproductive anatomy in Hershkovitz's marsupial publications are inaccurate and support the conclusion that his observations were cursory. For example, the statement that *Caluromysiops* and *Chironectes* differ from other didelphids by having a "simple" (undivided) glans penis (Hershkovitz, 1992b: 13) is not supported by any material that we have seen. Although a fluid-preserved adult male *Caluromysiops* that Hershkovitz examined (FMNH 60398) superficially appears to have an undivided penis because only one hemipene is extruded from the prepuce, the other half can be viewed by gently enlarging the preputial orifice with a probe. In fact, *Caluromysiops* and *Chironectes* have divided ("bifid") glandes like those of other didelphids.

phid tails differ taxonomically in shape and arrangement. Square or rectangular caudal scales in unambiguously annular series (state 0) occur in *Gracilinanus microtarsus*, *Marmosa canescens*, and *Thylamys*. Although individual cutaneous scales are indistinct in *Lestodelphys* and *Monodelphis*, we also scored those taxa with state 0 based on the annular arrangement of their caudal-hair triplets. By contrast, rhomboidal (diamond-shaped) or hexagonal scales in spiral series occur in *Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, *Marmosa lepida*, *M. murina*, *M. rubra*, *Marmosops*, *Micoureus*, and *Philander*. A few taxa, however, have caudal scales that appear to be morphologically intermediate between the annular and spiral morphotypes. In these taxa (*Metachirus*, *Marmosa mexicana*, *M. robinsoni*) the caudal scales appear to be in annular series over the vertebral articulations and in more-or-less spiral series elsewhere. In *Glironia*, the dorsal and lateral caudal surfaces are covered by body fur, and the entire ventral surface is modified for prehension (see da Silva and Langguth, 1989: fig. 1); therefore, no unmodified caudal scales are present in this taxon, for which we score the character as inapplicable ("-") in our matrix.

The shape and arrangement of didelphid caudal scales were coded as separate characters by Creighton (1984), but these are clearly not independent features. Rhomboidal scales cannot be efficiently packed around a cylinder in annular series, for example, nor can square scales be packed in spiral series (for illustrations, see Tate, 1933: fig. 2). Because caudal scale shape and packing geometry necessarily covary, and because scale arrangements are more easily characterized—despite the ambiguities recognized above—than scale shapes, we neither coded scale shape as a separate character nor included it in our state definitions. Since the three conditions defined above appear to represent a sequential series of transformations with state 1 as the obvious intermediate, we treated this character as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) in all of our analyses.

Character 24: *Unfurred ventral surface of tail base covered with smooth scales (0); or provided with raised tubercles (1).* The unfurred ventral surface of the tail base in most didelphids is covered by smooth flat scales, each of which is soft and flexible (yielding easily to the tip of a probe on fluid-preserved material). By contrast, the scales on the underside of the base of the tail are heavily cornified, forming hard raised tubercles in *Caluromys lanatus*, *Caluromysiops irrupta*, and *Glironia* (see da Silva and Langguth, 1989: fig 1a).

Character 25: *Ventral surface of tail tip covered by unmodified hair-bearing scales (0); or ventral surface of tail tip modified for prehension (1).* Although all didelphids are perhaps capable of caudal prehension to some extent, external morphological features associated with this behavior are variably developed in the family. The unfurred caudal surfaces of *Chironectes*, *Lestodelphys*, *Lutreolina*, *Metachirus*, and *Monodelphis* are covered with unmodified scales (each bearing three or more bristles) from base to tip. In taxa conforming to this morphology, the tail-tip may be provided with a smooth terminal button, but never with a ventrally expanded apical pad bearing dermatoglyphs. The tails of all other didelphids are provided with a distal prehensile surface that may be smooth or covered by modified scales (conspicuously unlike those of the caudal dorsum) but is always transversely creased and glabrous; in taxa conforming to this morphology, the tail-tip is invariably provided with a ventrally expanded pad bearing dermatoglyphs (da Silva and Langguth, 1989: fig 1b; Hershkovitz, 1997: fig. 7).

Creighton's (1984: character 19) coding of caudal prehensile modifications was based in part on the presence or absence of a median groove or sulcus, a distinction that we were unable to recognize consistently in our material. Additionally, his scoring of *Metachirus* and *Lutreolina* as indistinguishable from *Philander* and *Didelphis* in morphological traits associated with caudal prehension is inconsistent with our observations.

Character 26: *Caudal scales bearing three hairs each (0); or more than three hairs each (1).* Three hairs usually emerge from the posterior margin of each caudal scale in most didelphids, but four or more hairs usually emerge from each caudal scale in *Lutreolina* and *Philander*. Although individual cutaneous scales are often hard to dis-

tinguish in *Monodelphis*, the caudal hairs of species that we examined usually emerge from the skin in triplets, a condition that we interpreted as corresponding to state 0. Because the entire caudal dorsum is covered with body fur and the entire caudal ventrum is more-or-less glabrous and modified for prehension in *Glironia*, we were unable to code it for this character. We were also unable to confidently determine the state of this character in *Lestodelphys* based on the dried skins at hand. Both *Glironia* and *Lestodelphys* are therefore scored as missing ("?") in our matrix.

Creighton (1984: character 20) scored *Philander* as having three hairs per caudal scale, but our material of *P. frenata*, *P. mcilhennyi*, and *P. opossum* consistently exhibits four or more hairs per scale, the same condition described and illustrated for this genus by Hershkovitz (1997: 14, fig. 8). According to Creighton's text, only *Chironectes* and *Lutreolina* have more than three hairs per caudal scale, but his matrix (op. cit.: table 5) records this condition for *Lutreolina* and *Metachirus*. Four hairs emerge from beneath some ventral scales near the base of the tail in our material of *Chironectes*, but the modal count dorsally and distally is three in that genus, as it is in *Metachirus*.

Character 27: *Tail hairs emerging from each scale not grossly differentiated, varying in length but subequal in thickness (0); or central hair much thicker than lateral hairs (1).* The hairs that emerge from the posterior margin of each caudal scale are not grossly differentiated, varying in length but subequal in thickness, in most didelphids. However, in some species of *Marmosops* (including all of those sampled in this study), the middle hair of each caudal-scale triplet is conspicuously thicker than the lateral hairs, and it is often more darkly pigmented (Gardner and Creighton, 1989). *Glironia* could not be scored for this character for the reasons previously explained (see character 26).

Character 28: *Tail not incrassate (0); or incrassate (1).* The tail is a slender, muscular organ in most didelphids, but *Thylamys* and *Lestodelphys* have incrassate tails in which fat is seasonally deposited (Morton, 1980). Incrassate tails can be recognized superficially by their characteristically swollen, carrot-shaped outline and soft texture in fresh and fluid-preserved material, and by their flattened, grease-stained appearance in most skins.

Cranium and Mandible

The head skeleton is an important source of phylogenetically informative comparisons, but ontogenetic variation resulting from indeterminate postweaning growth must be taken into account when scoring didelphid characters (Abdala et al., 2001). Except as noted otherwise below, we determined character states of the skull and mandible from adult specimens, which we operationally defined as those with fully erupted permanent dentitions. Most of the material we examined was prepared for osteological study using dermestid beetles (Hall and Russell, 1933; Tiemier, 1940; Sommer and Anderson, 1974), a method that preserves even the most fragile bony structures (e.g., nasal tips, maxillary turbinals, ectotympanic rings, auditory ossicles) intact and in situ. By contrast, specimens prepared by boiling or maceration seldom retain all of the structures required for scoring the characters described below. With few exceptions, cranial nomenclature in the following accounts follows usages defined or referenced by Wible (1990) and Novacek (1993).

Character 29: *Premaxillae not produced anteriorly beyond I1 (0); or forming a distinct, shelf-like rostral process (1).* The premaxillae of many didelphids (*Caluromysiops*, *Chironectes*, *Didelphis*, *Glironia*, *Lestodelphys*, *Lutreolina*, *Marmosa canescens*, *Metachirus*, *Monodelphis*, *Philander*, and *Thylamys*) are short, terminating abruptly in front of the incisors, often without a definitive suture between the left and right elements (fig. 4B). In other didelphids, however, the premaxillae are produced anteriorly as a more-or-less acutely pointed shelf-like process that extends the bony rostrum beyond I1 and contains a distinct suture between the right and left bones (fig. 4A). Taxa that we scored as possessing a rostral process of the premaxillae include *Caluromys*, *Gracilinanus*, *Marmosa* (except *M. canescens*), *Micoureus*, and most examined species of *Marmosops*. The specimens of *Marmosops in-*

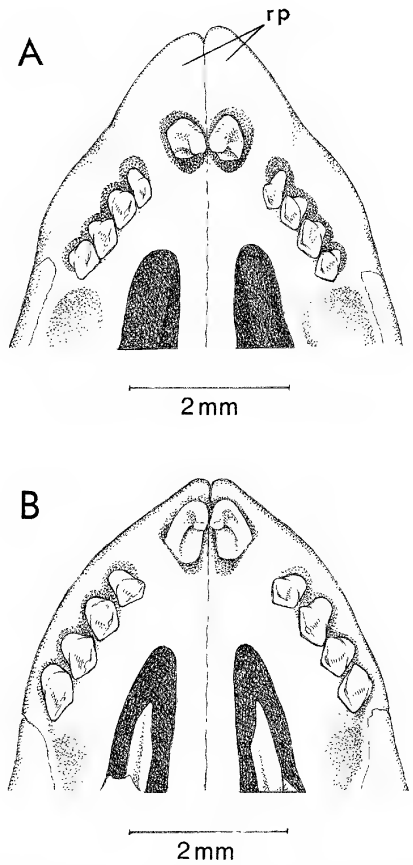

Fig. 4. Ventral view of rostrum in *Marmosa rubra* (**A,** MVZ 153280) and *Monodelphis brevicaudata* (**B,** AMNH 257203) illustrating taxonomic differences in premaxillary morphology. A broad, shelf-like rostral process (**rp**) extends the suture between right and left bones well anterior to the incisors in *M. rubra*, but the premaxillae form only narrow alveolar rims anterior to I1 in *M. brevicaudata*, where the left and right bones are separated by a small tissue-filled gap (not a distinct suture).

canus that we examined had oddly truncated premaxillae that might be preparation artifacts (the rostral process is sometimes damaged on carelessly prepared specimens, presumably when the nasal cartilages are cut in the last step of skin removal) or an intermediate condition between presence and absence, an uncertainty that we coded as a missing datum ("?").

Taxonomic variation in the shape of the premaxillae among didelphids has been noted by authors, notably Creighton (1984: character 33), who scored these bones as long (>1 mm) and "pointed" anterior to I1 only in the *murina* group of *Marmosa* (= *Marmosa* sensu stricto); other didelphid terminals in his analysis were scored as having short, rounded premaxillae. However, we did not observe that the premaxillae are consistently longer—or differently shaped—in *Marmosa* than in the other taxa scored as having a rostral process (state 1) in our matrix. Goin (1993) cited the possession of "shortened premaxillae" as synapomorphic for Caluromyidae, but undamaged specimens of both *Caluromys* species scored for this analysis have small but distinct rostral processes.

Character 30: *Premaxillae extend to upper canine alveoli (0); or upper canine alveoli contained entirely in maxillary bones (1).* A distinct palatal process of the premaxilla extends posteriorly to the upper canine alveolus on each side in most didelphids, but the palatal process is absent and C1 is contained entirely within the maxillary in *Caluromys* and *Caluromysiops*.

Character 31: *Maxilloturbinals large and elaborately branched (0); or small and unbranched (1).* The maxilloturbinals are thin, dorsally scrolling sheets of bone that occupy the lower part of the didelphid nasal fossa, where they arise from the inner surface of the maxilla on each side (for a general introduction to turbinal anatomy, see Moore, 1981). In most didelphids, the greater curvature of each maxilloturbinal scroll throws off secondary lamellae, which branch to form tertiary lamellae, which branch again to form an elaborate dendritic mass that presumably supports an extensive investing mucosa. By contrast, the maxilloturbinals are simple, slender, unbranched (or only sparsely ornamented) scrolls in all examined species of *Monodelphis*.

Character 32: *Nasal tips produced anteriorly above or beyond I1, obscuring nasal orifice in dorsal view (0); or posterior to I1, exposing nasal orifice dorsally (1).* The tips of the nasal bones are produced anteriorly to a point above or beyond I1 in most didelphids, and the nasal orifice is consequently not visible from a dorsal perspective. In *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*, however, the tips of the nasals do not

extend so far anteriorly, and the orifice is dorsally exposed.

Character 33: *Nasals conspicuously wider posteriorly than anteriorly (0); or nasals uniformly narrow, their lateral margins subparallel (1).* In most marsupials (and extinct metatherians) the nasals are much broader posteriorly (at or near the maxillary/premaxillary suture) than anteriorly. This phylogenetically widespread condition characterizes all didelphids scored for this analysis with the exception of *Marmosops incanus* (see Mustrangi and Patton, 1997: fig. 14) and *Thylamys* (see Flores et al., 2000: fig. 7), which usually have much narrower nasals with subparallel lateral margins.

Character 34: *Postorbital processes of frontals absent or indistinct (0); or present as flattened, wing-like extensions of supraorbital crests (1); or present but not flattened or associated with supraorbital crests (2).* Postorbital processes of the frontal bones are absent or indistinct in all examined adult specimens of *Gracilinanus*, *Lestodelphys*, *Marmosa rubra*, *Marmosops*, *Metachirus*, *Monodelphis*, and *Thylamys*, Although postorbital processes are commonly reported as present (without any qualifying descriptor) among other didelphid taxa, we distinguish two distinct morphologies of postorbital frontal outgrowths. In *Caluromys*, *Caluromysiops*, *Glironia*, *Marmosa* (except *M. rubra*), and *Micoureus*, the postorbital processes are flattened and more-or-less triangular projections of the supraorbital crests that shield the dorsal margin of the eye cavity. By contrast, the postorbital processes in *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* are bluntly pyramidal or horn-like projections that are not associated with supraorbital crests. Because frontal outgrowths develop late in postweaning ontogeny (Abdala et al., 2001), it is important that this character be scored from examination of large adult skulls. As none of the observed states of frontal morphology appear to be obviously intermediate to the others, this character was treated as unordered in our analysis.

Character 35: *Scars of M. temporalis origin on braincase not fused middorsally to form sagittal crest, or sagittal crest small, not extending to frontals (0); or sagittal crest large and extending to frontals (1).* In most didelphids the right and left scars of origin of M. temporalis are widely separated on the braincase, and no sagittal crest is developed. In large adult specimens of *Caluromys*, *Lestodelphys*, and *Monodelphis*, however, a small sagittal crest is sometimes developed over the interparietal or along the midparietal suture. Because such small crests are often indistinct, we include the entire range of variation (from unambiguous absence to small) as a single state. By contrast, much larger sagittal crests that extend anteriorly along the midfrontal suture—an unambiguously different condition—are consistently developed in adult specimens of *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*.

Character 36: *Parietal and alisphenoid in contact on lateral aspect of braincase (0); or no parietal-alisphenoid contact (1).* Among marsupials and extinct metatherians, either the parietal and alisphenoid are in contact on the lateral surface of the braincase, or those bones are separated by contact between the frontal and squamosal (Archer, 1976a; Marshall and Muizon, 1995; Muizon, 1998). Parietal-alisphenoid contact is exhibited by all of the didelphids we examined with the unique exception of *Metachirus*, in which the frontal and squamosal are in contact as previously reported by Wroe et al. (2000: character 64). Kirsch and Archer (1982: character 28) incorrectly scored *Metachirus* as resembling other didelphids in this trait.

Character 37: *Petrosal not exposed on lateral aspect of braincase (0); or polymorphic (1); or consistently exposed laterally by fenestra between squamosal and parietal bones* (2). In most didelphids, the petrosal is only exposed on the occiput (where it is bounded by the squamosal, exoccipital, and supraoccipital) and ventrally (between the exoccipital, basioccipital, and alisphenoid; see Wible, 1990: fig. 1). In taxa conforming to this morphology (*Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Glironia*, *Lutreolina*, *Marmosa*, *Metachirus*, *Micoureus*, *Monodelphis*, *Philander*), there is no petrosal exposure through openings on the lateral surface of the braincase. By contrast, the petrosal capsule that encloses the paraflocculus and semicircular canals (= pars canalicularis or pars mastoideus) is consistently exposed through a fenestra in the suture between the

squamosal and parietal in *Gracilinanus*, *Thylamys*, and some species of *Marmosops*. Both conditions occur as polymorphisms (neither state clearly predominating) in *Lestodelphys*, *Marmosops incanus*, and *M. noctivagus*. For *Marmosa lepida* we coded the unambiguously modal condition (no lateral petrosal exposure) despite a single specimen (MNHN 1998–306) with a distinct fenestra in the squamosal-parietal suture on both sides of the skull. As for other transformation series involving polymorphic states, we treated this character as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) in all of our analyses with transformations between adjacent states assigned a parsimony cost of 0.5.

Character 38: *Maxillopalatine fenestrae consistently absent or indistinct (0); or polymorphic (1); or large and distinct (2).* Marsupial palatal fenestrations have often been discussed in a phylogenetic context, but homoplasy and variability rather than homology and taxonomic consistency have been emphasized by most authors (e.g., Marshall, 1979; Reig et al., 1987). Reservations about coding fenestral characters for phylogenetic analysis are certainly appropriate if taxonomic comparisons are not ontogenetically standardized,[6] or if palatal openings are simply scored as present or absent without reference to anatomical location (as by Kirsch and Archer, 1982: character 48; Reig et al., 1987: character 27; Wroe et al., 2000: character 47). Although distinct fenestral loci have long been recognized by taxonomists (e.g., Tate, 1933; Archer, 1981; Hershkovitz, 1992b), inconsistent terminology makes it difficult to recognize homologies among the conditions described by different authors. The fenestral nomenclature adopted in this report is illustrated in figure 5.

Among didelphids, only *Caluromysiops* and *Caluromys* lack consistently well-formed maxillopalatine fenestrae. Small perforations in the maxillary-palatine sutures occur in most examined specimens of both genera (see Izor and Pine, 1987: fig. 1), but these appear to be vascular openings and do not resemble the larger, obviously nonvascular fenestrae of other didelphids. Archer (1982) and Reig et al. (1987) reported that *Glironia* lacks palatal fenestrations, but distinct maxillopalatine openings (illustrated by Marshall, 1978b: fig. 2) are present in some adult specimens of this rare taxon, which we coded as polymorphic. Maxillopalatine fenestrae are unambiguously present in all of the remaining didelphids that we examined. As for other transformation series involving polymorphisms, we treated this character as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) in all of our analyses with transformations between adjacent states assigned a parsimony cost of 0.5.

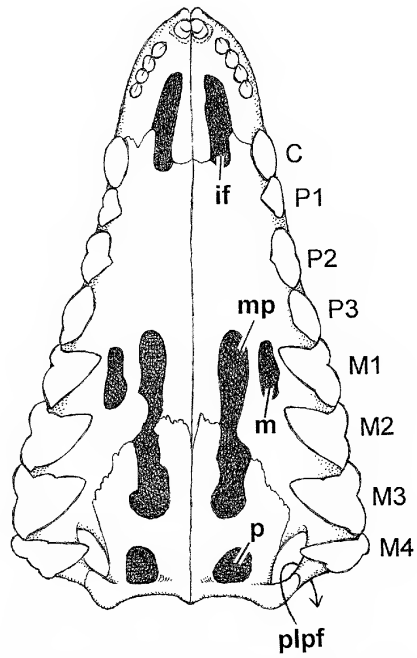

Fig. 5. Palatal morphology of *Thylamys venustus* (AMNH 261254) illustrating nomenclature for fenestrae and foramina described in the text. The maxillary dentition (C–M4) provides convenient landmarks for defining the size and position of palatal perforations. Abbreviations: **if,** incisive foramen; **m,** maxillary fenestra; **mp,** maxillopalatine fenestra; **p,** palatine fenestra; **plpf,** posterolateral palatal foramen.

Character 39: *Palatine fenestrae absent (0); or present (1).* Many didelphids have, in

[6] At least some didelphid palatal fenestrations are apparently formed by resorption of bone in postweaning ontogeny (Abdala et al., 2001), so only adult specimens provide a reliable basis for taxonomic comparisons and character-state coding. Although individual differences in the occurrence of small fenestrae can sometimes be observed in large samples of conspecific adults, such variability appears no greater than that seen in other craniodental traits commonly analyzed for phylogenetic content.

addition to maxillopalatine fenestrae, separate openings in the posterior palate that are entirely contained within the palatine bones. Palatine fenestrae are consistently present in adult specimens of *Didelphis*, *Gracilinanus*, *Lutreolina*, *Marmosa mexicana*, *Philander*, *Thylamys*, and some species of *Marmosops* (e.g., *M. impavidus*, *M. incanus*). Presence is also the modal condition for *Lestodelphys* and *Marmosops noctivagus*, in which individuals without palatine perforations appear to be uncommon variants. Palatine fenestrae are consistently absent in *Caluromys*, *Caluromysiops*, *Chironectes*, *Glironia*, *Metachirus*, *Monodelphis*, some species of *Marmosops* (e.g., *M. parvidens*, *M. pinheiroi*), and most species of *Marmosa* and *Micoureus*. Absence is the modal condition for *Marmosops pinheiroi* and *Micoureus paraguayanus*, in which a single specimen each exhibited small unilateral palatine perforations.

Character 40: *Maxillary fenestrae absent (0); or present (1).* Most didelphids with fenestrated palates have only maxillopalatine or maxillopalatine and palatine openings. A few species, however, have additional fenestrae that are located in the maxillary bone between the maxillopalatine fenestra and the toothrow (at the level of M1 or M2) on each side of the palate. Maxillary fenestrae are consistently present in *Gracilinanus microtarsus* and *Marmosa canescens*, and presence is also the modal condition in our material of *Thylamys venustus*. All other didelphid taxa in our study consistently lack maxillary vacuities except as rare unilateral variants. Creighton (1984: character 26) referred to these openings as "mesolateral" or "mediolateral" fenestrae and noted that they are sometimes confluent with the maxillopalatine fenestrae in *Marmosa canescens*. Our observations are consistent with his remarks, but it does not seem necessary to create an additional state for the confluent morphology that is variably expressed in that species.

Character 41: *Posterolateral palatal foramina posterior to fourth molars (0); or extending lingual to M4 protocones (1).* In all didelphids—and many other metatherians—a large foramen perforates the maxillary-palatine suture posterolingual to the molar row on each side. According to Archer (1976a), this foramen transmits the minor palatine artery from the maxillary artery to the ventral surface of the palate. In most didelphids the posterolateral palatal foramina are small and located behind the fourth molar (fig. 6), but these openings are conspicuously larger and extend anteriorly lingual to the protocone of M4 on each side in *Lestodelphys* and *Thylamys* (fig. 5). Creighton (1984: character 24) referred to these openings as "posterolateral fenestrae" and defined their size with respect to the width of M4, but the dimensions of that tooth exhibit independent taxonomic variation that we prefer to score as a separate character (below). Published illustrations of the skull of *Lestodelphys* (see Marshall, 1977: fig. 1; Reig et al., 1987: fig. 50) depict the posterolateral foramina as posterior to M4, but in all of the specimens we examined the foramina conform to state 1 as described above.

Character 42: *Posterior palate gently sloping ventrally, usually with arched caudal margin and without prominent corners, choanae unconstricted behind (0); or abruptly inflected ventrally, with approximately straight caudal margin and prominent lateral corners, choanae constricted (1).* Two alternative morphologies of the posterior palate and the internal choanae can be recognized among didelphids. In caluromyines (*Caluromys*, *Caluromysiops*, *Glironia*) the posterior palate slopes ventrally without any abrupt inflection, the caudal palatal margin is usually broadly arched, and prominent lateral corners are not developed; behind the palate, the internal choanae are not strongly constricted (fig. 6A). By contrast, the posterior palate of didelphines is abruptly inflected ventrally, and the caudal palatal margin is more-or-less straight with prominent lateral corners; behind the palate, the choanae are strongly constricted (fig. 6B). Rather than scoring each of these transformations (slope of the palatal roof, shape of the palatal margin, etc.) separately, we recognize a pattern of correlated changes that appears to involve a reorientation of the oral airway. Although some examined individuals of species scored with either condition differ in minor details (e.g., in some specimens otherwise conforming to state 1 the posterolateral palatal corners are less strongly produced than in others), the overall pattern of posterior palatal

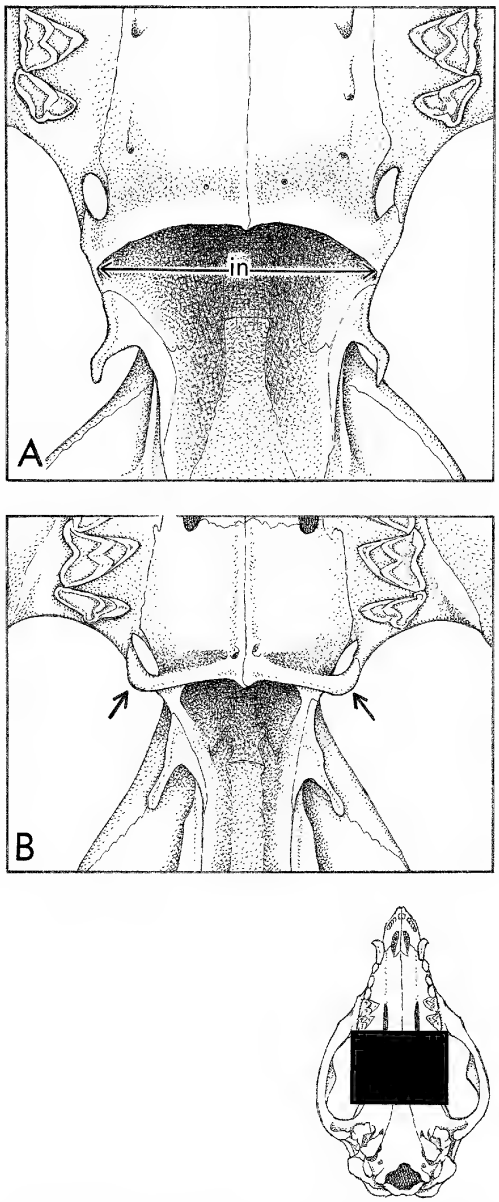

Fig. 6. Ventral midcranial view of *Caluromys philander* (**A,** AMNH 267002) and *Micoureus demerarae* (**B,** AMNH 266428) illustrating taxonomic differences in palatal morphology. In caluromyines the posterior palate slopes gently ventrally, and the palatal margin is arched (concave posteriorly) without strongly projecting lateral corners; the internal nares (**in**) are very broad. In didelphines, however, the posterior palate is abruptly inflected ventrally and the palatal margin is more-or-less straight with projecting lateral corners (arrows in lower panel); the internal nares are narrow.

morphology is distinctly recognizable in all of the taxa examined for this analysis.

Character 43: *Maxillary and alisphenoid separate (0); or in contact on orbital floor (1).* The maxillary and alisphenoid do not contact one another in most didelphids, although these bones are often closely approximated on the floor of the orbit (fig. 7A). By contrast, the maxillary and alisphenoid are consistently in contact on the orbital floor of *Lutreolina* and *Monodelphis* (fig. 7B). In occasional specimens of some taxa that do not otherwise exhibit maxillary-alisphenoid contact (e.g., *Chironectes*, *Marmosa murina*, *Metachirus*, *Philander mcilhennyi*) a thread-like process of the maxillary narrowly contacts the alisphenoid (often unilaterally), but we did not score such uncommon variants as polymorphisms.

Character 44: *Transverse canal foramen absent (0); or present (1).* A foramen that transmits the venous transverse canal is present anterolateral to the carotid foramen in many marsupials and extinct metatherians (Sánchez-Villagra, 2001; Sánchez-Villagra and Wible, 2002). The typical didelphid condition (presence) is clearly depicted by Wible (1990: fig. 1), but the transverse canal foramen is sometimes incorrectly identified in other published illustrations of didelphid skulls (e.g., by Hershkovitz [1992b: fig. 18; 1997: fig. 11], who mislabeled it as the "foramen rotundum").[7] *Caluromys* and *Caluromysiops*, however, lack a transverse canal foramen (Archer, 1976a; Sánchez-Villagra and Wible, 2002). According to Kirsch and

[7] Because Hershkovitz's publications on didelphid systematics are profusely illustrated and widely consulted for anatomical information, it should be recognized that some basicranial foramina are misidentified in his figures. In addition to the problem noted above, the carotid foramen (= anterior carotid foramen of Wible, 1990: fig. 1) is often labeled as the "foramen ovale," the foramen ovale as the "anterior lacerate foramen or petrotympanic fissure," and the secondary foramen ovale as the "carotid foramen or canal" (Hershkovitz, 1992b: fig. 18; 1997: fig. 11; 1999: figs. 7, 25). Confusingly, these misidentifications are not consistent. For example, the opening labeled as the foramen rotundum on each side of the skull in other figures (e.g., Hershkovitz, 1999: fig. 25) is a nonvascular fenestra rather than the transverse canal foramen, but the foramen rotundum is sometimes correctly labeled in figures adjacent to those in which it is not (e.g., Hershkovitz, 1992b: fig. 19; 1997: fig. 12).

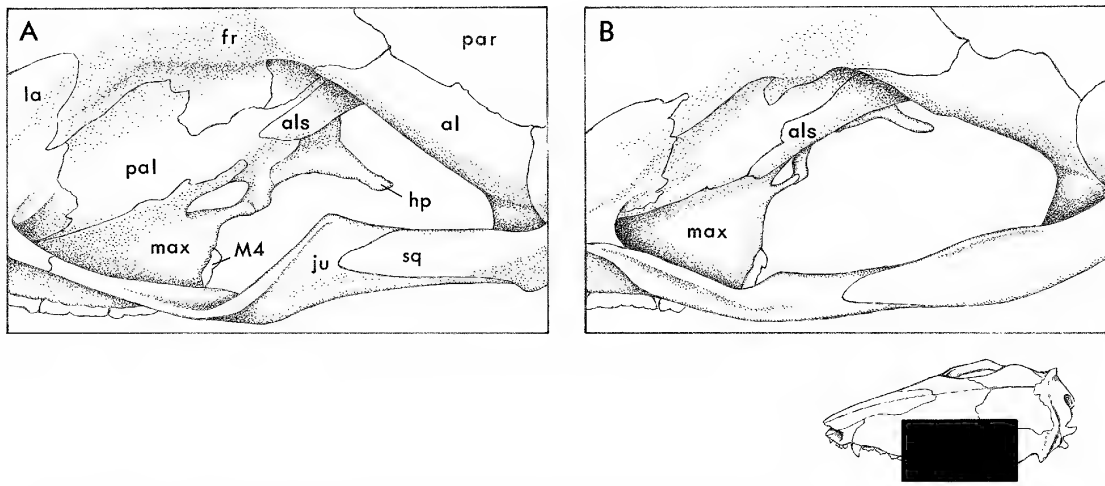

Fig. 7. Oblique dorsolateral view of the left orbit in *Thylamys venustus* (**A,** AMNH 263562) and *Monodelphis adusta* (**B,** AMNH 272695) illustrating taxonomic differences in sutural patterns. In *Thylamys* (and most other didelphids), the maxillary (**max**) and alisphenoid (**als**) bones are separated by the palatine (**pal**), but the alisphenoid extends anteriorly across the palatine to contact the maxillary in *Monodelphis*. Other osteological abbreviations: **fr,** frontal; **hp,** hamular process of pterygoid; **ju,** jugal; **la,** lacrimal; **par,** parietal; **sq,** squamosal.

Archer (1982: character 24), the "transverse canal" is absent in *Metachirus nudicaudatus* and *Philander opossum*, but all of the specimens we examined of both taxa had a transverse canal foramen on each side of the skull. The transverse canal foramen is occasionally present unilaterally, and it is absent on both sides of the skull in rare examples of some species that otherwise consistently exhibit these openings. Rather than code such infrequent variation as polymorphisms, we scored the modal condition (presence or absence) for each didelphid terminal in our analysis. Sánchez-Villagra and Wible (2002) analyzed the presence or absence of an intramural connection between the left and right transverse canal foramina in their recent survey of didelphid basicranial characters, but confident scoring of this feature requires sectioned or suitably broken skulls, which were not available for the large majority of taxa included in our study.

Character 45: *Extracranial course of mandibular nerve not enclosed by bone (0); or consistently enclosed by anteromedial strut of alisphenoid bulla (1); or usually enclosed by posteromedial bullar lamina (2).* The openings through which the mandibular division of the trigeminal nerve (V^3) exits the skull have been variously named by systematists. Following Gaudin et al. (1996), we use the term "foramen ovale" for the primary orifice through which V^3 exits the endocranial lumen of the adult skull. In most didelphids, the foramen ovale is bordered by the alisphenoid and the petrosal (fig. 8A), but the foramen is sometimes contained entirely within the alisphenoid, and both conditions

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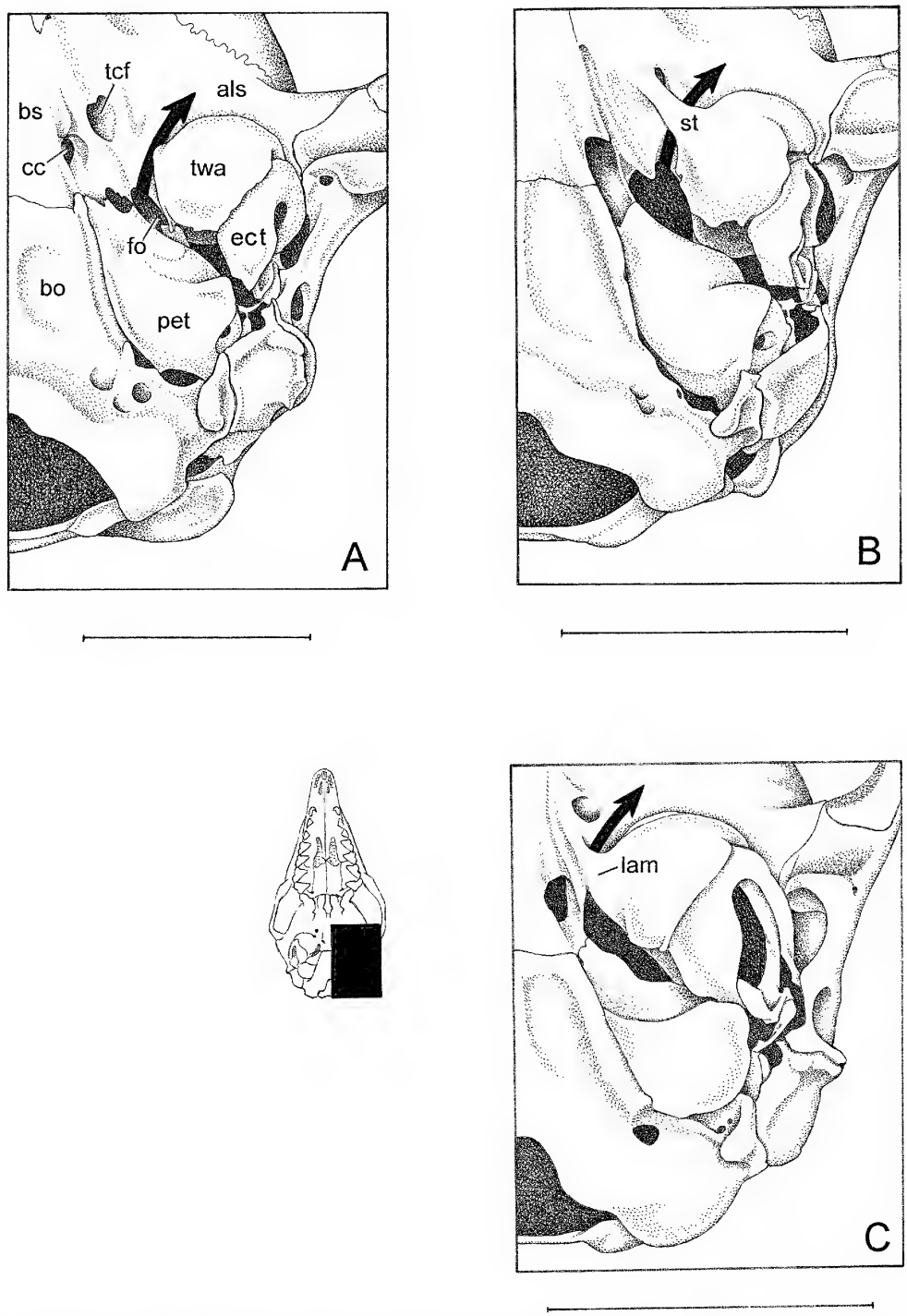
Fig. 8. Ventral view of left ear region in *Marmosa murina* (**A,** AMNH 267368), *Marmosops pinheiroi* (**B,** AMNH 267346), and *Monodelphis theresa* (**C,** MVZ 182775) illustrating taxonomic differences in secondary foramen ovale formation. In *Marmosa*, the mandibular branch of the trigeminal nerve (V^3, reconstructed course shown by heavy arrow) emerges from the endocranial lumen via the foramen ovale (**fo**), which is bordered by the alisphenoid (**als**) and the petrosal (**pet**); the extracranial course of the nerve is unenclosed in this taxon. In *Marmosops*, however, the extracranial course of V^3 is partially enclosed by a bony strut (**st**) that extends from the anteromedial surface of the tympanic



wing of the alisphenoid (**twa**) across the transverse canal foramen (**tcf**); the nerve then emerges from a so-called secondary foramen ovale. Another kind of secondary enclosure is seen in *Monodelphis*, where the nerve emerges from a secondary foramen ovale formed by a medial lamina (**lam**) of the alisphenoid tympanic wing. Other abbreviations: **bs,** basisphenoid; **bo,** basioccipital; **cc,** carotid canal; **ect,** ectotympanic.

can be seen on opposite sides of the same skull (see Gaudin et al., 1996: fig. 6). Because it is often difficult to determine the position of this opening with respect to relevant endocranial sutures, however, we did not score the position of the foramen ovale per se. Instead, secondary enclosures of V^3 by outgrowths of the alisphenoid tympanic wing provide a more accessible basis for taxonomic comparisons.

Gaudin et al. (1996) distinguished three states of secondary enclosure of the mandibular nerve by alisphenoid outgrowths among marsupials: absence (no secondary enclosure), incomplete enclosure (presence of a secondary foramen but no canal), and complete enclosure (presence of a canal continuous with the primary foramen). Among didelphids, however, there are two different (apparently nonhomologous) conditions of secondary nerve enclosures that are not distinguished by this coding scheme.

In juveniles and adults of *Gracilinanus*, *Lestodelphys*, *Marmosops*, *Metachirus*, and *Thylamys* the extracranial course of V^3 is enclosed by an alisphenoid process or strut that arises from the anteromedial surface of the bulla and extends anteriorly, medially, and dorsally to span the transverse canal foramen. In the smaller species with this condition (e.g., *Marmosops pinheiroi*; fig. 8B) the extracranial course of V^3 remains unenclosed between this process and the primary foramen ovale, but in larger species (e.g., *Marmosops noctivagus*) a sheet of bone produced from the posterior edge of the process extends caudally to form a more-or-less complete canal late in postnatal life.

The alternative pattern of secondary foramen and canal formation (state 2) is seen in *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, *Monodelphis theresa*, and *Philander*. In these taxa, V^3 is broadly enclosed by an alisphenoid lamina (fig. 8C) that extends along the posteromedial bullar surface, but there is no anteromedial process spanning the transverse canal foramen. Many juvenile specimens of some taxa scored with this condition (e.g., *Didelphis*) do not have a fully enclosed secondary foramen and canal, but they usually show some laminar development; subadults and young adults show progressively more complete enclosure; and old adults (large specimens with heavily worn teeth) usually have completely enclosed foramina and canals (Abdala et al., 2001). All other didelphid taxa examined for this analysis (*Caluromys*, *Glironia*, *Marmosa*, *Micoureus*, *Monodelphis adusta*, *M. brevicaudata*, *M. emiliae*) lack secondary enclosures of the mandibular nerve except as rare (usually unilateral) variants.

We treat this character as unordered, an analytic option consistent with our hypothesis that the two kinds of secondary enclosures described above are nonhomologous alternative conditions.

Character 46: *Anterior limb of ectotympanic directly attached to skull (0); or indirectly attached via malleus (1).* Although didelphids were described by van der Klaauw (1931: 26) as having a completely free ectotympanic, two distinct patterns of attachment can be recognized in the family. In most didelphids (*Glironia*, *Gracilinanus*, *Lestodelphys*, *Marmosa*, *Marmosops*, *Metachirus*, *Micoureus*, *Monodelphis*, *Thylamys*) the anterior (dorsal) limb of the ectotympanic (tympanic annulus) is directly connected to the skull near the point where the squamosal, alisphenoid, and petrosal are juxtaposed behind the postglenoid process. Where the connection can be seen clearly (dried remnants of soft tissues frequently obscure this feature), the actual attachment usually seems to be to the petrosal (fig. 9A). Alternatively (in *Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*), the anterior limb of the ectotympanic is not directly attached to the skull, and the suspension of the tympanic annulus is indirect, via the tympanic (anterior) process of the malleus (fig. 9B).

In all examined taxa with an indirect dorsal connection between the ectotympanic and the skull (state 1), the tympanic annulus is more-or-less ringlike because the posterior (ventral) limb is not expanded medially to form part of the floor of the middle ear cavity. By contrast, in taxa with direct ectotympanic suspension, the posterior limb tends to be dorsoventrally flattened and medially expanded, forming part of the bullar floor to a greater or lesser extent. This aspect of taxonomic variation in ectotympanic morphology, obviously correlated with the suspensory difference scored herein, was previously cod-

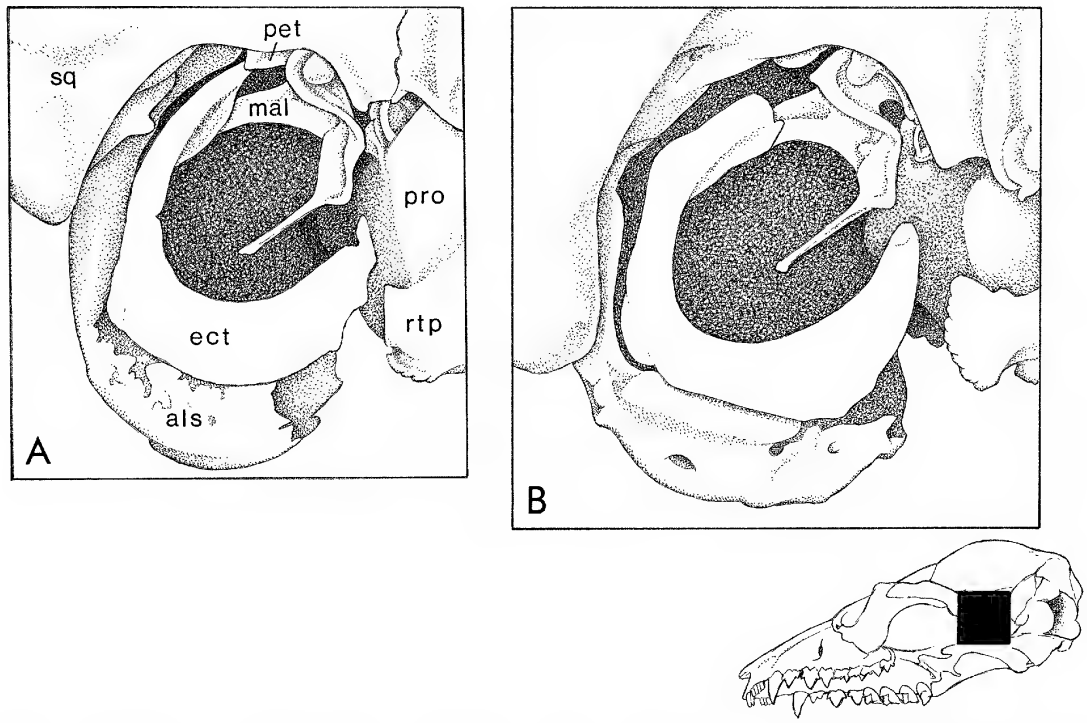


Fig. 9. Oblique ventrolateral view of left ear region in *Marmosops impavidus* (**A,** MUSM 13284) and *Philander mcilhennyi* (**B,** MUSM 13299) illustrating taxonomic differences in ectotympanic suspension. Whereas the ectotympanic (**ect**) is suspended from the skull by attachments both to the petrosal (**pet**) and to the malleus (**mal**) in *Marmosops*, the ectotympanic of *Philander* is suspended only from the malleus (there is no attachment to the petrosal). Other abbreviations: **als,** alisphenoid; **pro,** promontorium; **rtp,** rostral tympanic process (of petrosal); **sq,** squamosal.

ed for phylogenetic analysis by Kirsch and Archer (1982: character 52), Creighton (1984: character 28), Reig et al. (1987: character 31), and Goin and Rey (1997: character 11), but their discrepant observations (e.g., regarding *Metachirus* and *Monodelphis*) reflect the difficulty of unambiguously distinguishing degrees of ectotympanic expansion, or (perhaps) differences in the species-level exemplars chosen to represent generic terminals in those analyses (see Jansa and Voss, 2000: 70–71).

Character 47: *Fenestra cochleae of petrosal exposed in lateral or ventrolateral view (0); or fenestra concealed within a sinus formed by the caudal and rostral tympanic processes (1).* In most didelphid and extinct metatherian petrosals, the fenestra cochleae is completely exposed in lateral or ventrolateral view (as illustrated for *Didelphis* by Wible, 1990: fig. 1). In *Caluromys*, *Caluromysiops*, *Lestodelphys*, *Marmosa rubra*, *Monodelphis emiliae*, and *Thylamys*, however, the fenestra cochleae is concealed within a chamber or sinus formed by a laminar outgrowth of the pars canalicularis that approximates or contacts an expanded rostral tympanic process of the pars cochlearis. This lamina, which appears to be homologous with the caudal tympanic process of MacPhee (1981), is invariably fused posteroventrally with the paroccipital process (of the exoccipital), which also throws forward a small "tympanic" outgrowth. Wroe et al. (2000: characters 66, 67) coded what appears to be the same taxonomic variation as two characters (one each for the "paroccipital tympanic process" and the "mastoid tympanic process"), but only a single anatomical transformation (sinus formation) is apparent to us among the taxa included in this study. Sánchez-Villagra and Wible (2002) recorded

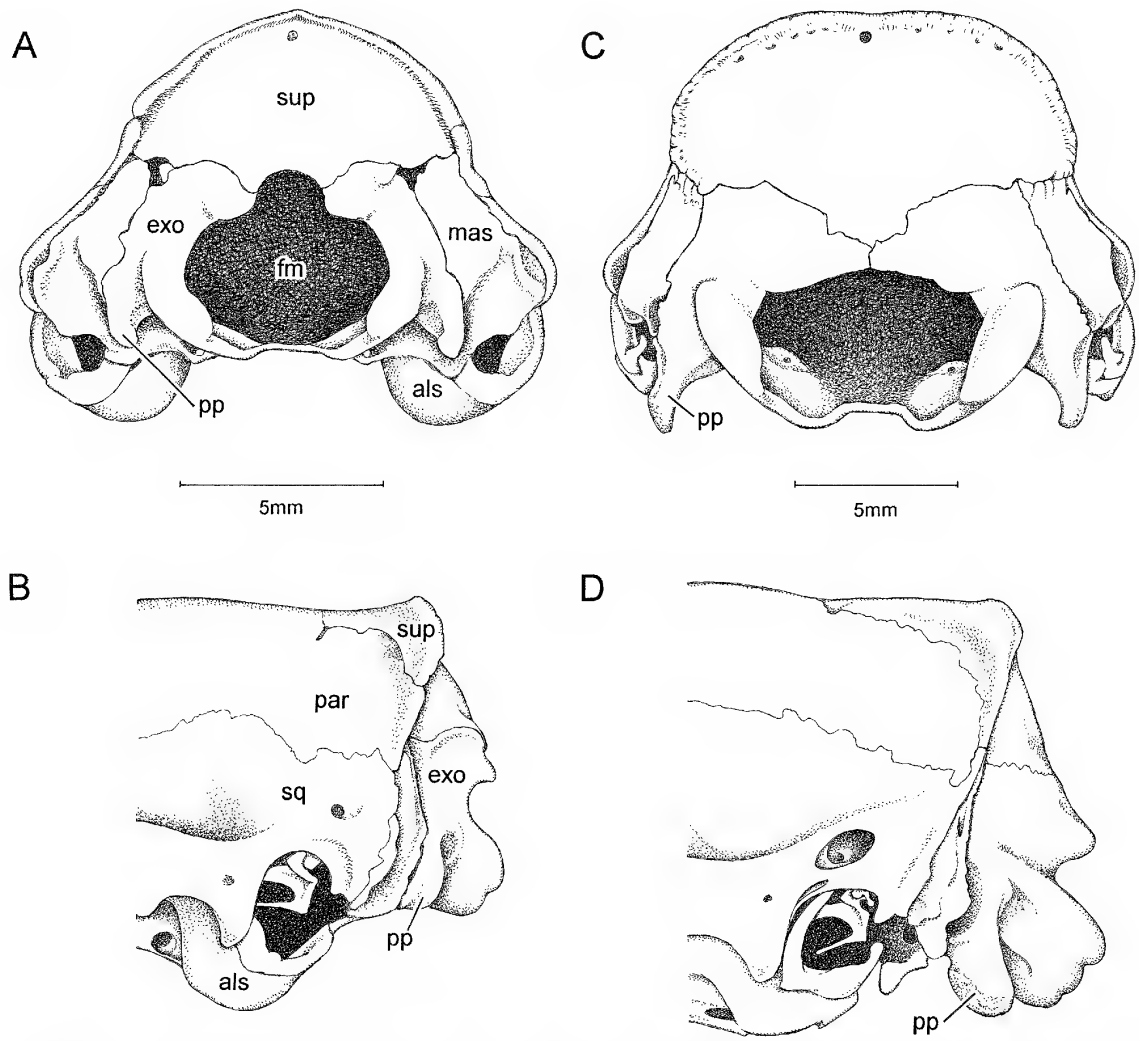


Fig. 10. Posterior and lateral views of the occipital region in *Lestodelphys halli* (**A, B,** UWZM 22422) and *Metachirus nudicaudatus* (**C, D,** AMNH 267009). In *Lestodelphys* the dorsal margin of the foramen magnum (**fm**) is formed by the excoccipitals (**exo**) and the supraoccipital (**sup**), but in adult specimens of *Metachirus* the right and left exocciptals are joined to exclude the supraoccipital from the dorsal margin of the foramen. Another conspicuous taxonomic difference illustrated in these views concerns the paroccipital process (**pp**), which is a small, inconspicuous bony mass adnate to the pars mastoideus (**mas**) of the petrosal in *Lestodelphys*. By contrast, the paroccipital process of *Metachirus* is much larger and projects almost straight ventrally. Other abbreviations: **als,** alisphenoid tympanic wing; **par,** parietal; **sq,** squamosal.

contact between the caudal and rostral tympanic processes in *Lestodelphys* and *Thylamys*, but did not observe such contact in the other taxa listed above.

Character 48: *Paroccipital process small and rounded or subtriangular, its base broadly adnate to the petrosal and its apex directed posteroventrally (0); or a large erect process usually directed ventrally (1).* The paroccipital process of the exoccipital is inconspicuous in most didelphids, consisting of a low, rounded or subtriangular bony mass for muscle attachment that is broadly adnate to the petrosal; the indistinct apex of the process in taxa that conform to this widespread condition is directed posteroventrally (fig.

10A, B). By contrast, in *Chironectes*, *Didelphis*, *Lutreolina*, *Metachirus*, and *Philander* the paroccipital process is much larger, more erect, and points almost straight ventrally in most examined specimens (fig. 10C, D).

Kirsch and Archer (1982: character 51) coded the paroccipital process as "long" in most of the didelphids included in their analysis (*Caluromys*, *Chironectes*, *Didelphis*, *Glironia*, *Lutreolina*, *Marmosa*, *Metachirus*, *Monodelphis*, *Philander*) versus "very small but not absent" in *Lestodelphys*. However, we were not able to distinguish any aspect of paroccipital morphology that corresponded to their pattern of taxonomic scoring in our material. Instead, the condition of the paroccipital process in *Lestodelphys* appeared to be indistinguishable from the widespread morphology among small didelphids, which includes a modest range of intergrading forms but not the hypertrophied state seen in *Metachirus* and the $2n = 22$ opossums.

Rougier et al. (1998) and Wible et al. (2001) used the term "paracondylar" for the muscular process of the exoccipital (after Evans and Christensen, 1979),[8] reserving "paroccipital" for a muscular process of the petrosal, but our usage follows Coues (1872), Flower (1885), and most other works of comparative mammalian osteology. That the two structures are homologous (as bony sites for muscle attachment) is suggested by the fact that no taxon scored by Rougier et al. (1998) and Wible et al. (2001) for the "paracondylar" character (number 135 in their matrix) and for the paroccipital character (number 131) was observed to have both processes. On this hypothesis, future analyses of basal therian relationships should include one character for presence/absence of a paroccipital process and another for its position (on the petrosal or exoccipital).

Character 49: *Dorsal margin of foramen magnum formed by exoccipitals and supraoccipital (0); or by exoccipitals only (1).* The dorsal margin of the foramen magnum is formed by the exoccipitals and the supraoccipital in most didelphids (fig. 10A), but medial processes of the left and right exoccipitals are joined at the midline above the foramen magnum (excluding the supraoccipital from the dorsal margin of that opening; fig. 10C) in adult specimens of *Didelphis*, *Lutreolina*, *Metachirus*, and *Philander*. Juvenile (and some subadult) specimens of these four genera, however, resemble other didelphids in their occipital morphology, such that both states can be observed in ontogenetic series of conspecific skulls (see Abdala et al., 2001: fig. 3). Sánchez-Villagra and Wible (2002) coded *Chironectes* as exhibiting the same morphology as the four genera listed above, but the supraoccipital forms part of the dorsal margin of the foramen magnum in all of the ten specimens of *Chironectes* that we examined for this character (not all of the adult skulls listed in appendix 1 have visible occipital sutures). The unusual and obviously derived condition that we code as state 1 was apparently first described by Coues (1872), but seems to have remained unremarked by subsequent comparative anatomists until scored for phylogenetic analysis by Rougier et al. (1998).

Character 50: *Mandible with two mental foramina (0); or with only one (1).* Most didelphids have two mental foramina that perforate the lateral surface of the mandible, of which the more anterior is usually larger and located below p1 or p2, and the more posterior is usually smaller and located below p3 or m1 (Tate, 1933: fig. 6). *Chironectes*, however, consistently exhibits only a single mental foramen, which is very large and occupies the same position as does the anterior foramen in those taxa with two lateral mandibular perforations.

Character 51: *Angular process acute (more-or-less pointed) and strongly inflected (0); or obtuse (bluntly rounded) and weakly inflected (1).* Alternative states of the form and orientation of the marsupial angular process were defined by Sánchez-Villagra and Smith (1997), but we were unable to consistently recognize the distinction between the "rod-like" and "intermediate" conditions they scored for didelphid exemplars. Instead,

[8] The term "paracondylar process" occurs in just one illustration in Evans and Christensen (1979: fig. 4–9), but the accompanying text refers to this structure as the "jugular process", and it is so labeled in other illustrations (op. cit.: figs. 4–38, 4–39); the index contains an entry for the jugular process, but none for a paracondylar process. Although a "processus paracondylaris" is illustrated in at least one textbook on veterinary anatomical nomenclature (Schaller, 1992: 17), no established zoological usage for this neologism appears to exist.

both rod-like and intermediate angular processes are here combined as "acute and strongly inflected", a condition common to most didelphids. Only *Caluromys* and *Caluromysiops* have bluntly rounded and weakly inflected mandibular angles. Sánchez-Villagra and Wible (2002) also treated this character as binary and recorded the same taxonomic variation that we recognize, but coded the medial inflection of the mandibular angle as "present" (state 0) or "absent" (state 1).

Dentition

Metatherian dental homologies have been the topic of past controversy, but most recent authors (e.g., Marshall and Muizon, 1995; Hershkovitz, 1997; Rougier et al., 1998; Wroe et al., 2000; Voss et al., 2001) have agreed with Flower (1867) and Luckett (1993) that the replaced molariform tooth of the upper and lower jaw is the deciduous third premolar (dP3/dp3), and that no anterior premolars are missing. Therefore, the 14 postcanine teeth of adult didelphids appear to be P1/p1, P2/p2, P3/p3, M1/m1, M2/m2, M3/m3, and M4/m4.[9] The nomenclature for molar occlusal structures mentioned in the following accounts is illustrated by Bown and Kraus (1979: fig. 9–1) and by Reig et al. (1987: fig. 1). References for other dental terminology are cited as necessary below. Occlusal features that are easily distinguished on unworn juvenile or subadult dentitions are often obliterated by wear in adults; therefore, we scored most of the following characters from immature specimens. The exceptions are relative height comparisons involving P3 or p3 (the last teeth to erupt in most didelphids), which we scored from adult material.

Character 52: *I2–I5 with approximately symmetrical, rhomboidal crowns (0); or with conspicuously asymmetrical crowns (1).* The upper first incisor (I1) of all didelphids is a more-or-less styliform tooth, conspicuously unlike I2–I5, and usually set apart from them by a small diastema. Although authors have remarked taxonomic differences in the degree of hypsodonty of I1, such variation appears to be continuous rather than discrete among the numerous terminals included in our analysis. Instead, phylogenetically useful variation in incisor morphology is more easily scored for the more posterior teeth in this series.

The crowns of I2–I5 are approximately symmetrical rhomboids in most didelphids, with subequal anterior (mesial) and posterior (distal) cutting edges that converge to form a sharp central apex; usually, a distinct anterior angle (mesiostyle) and a posterior angle (distostyle) can be seen on unworn teeth (fig. 11A). This is the morphology that Takahashi (1974: 414) labeled "premolariform", as exemplified by *Monodelphis*, *Marmosa*, and *Metachirus* in her study. In many taxa with posterior upper incisors of this type, the tooth crowns increase in breadth (antero-posterior or mesio-distal dimension) from front to back, such that I2 appears visibly smaller than I5 in labial view. This tendency (which was coded for phylogenetic analysis by Creighton, 1984: character 43) is very pronounced in some taxa with premolariform incisors (e.g., *Micoureus*, *Marmosops*, *Metachirus*) but seems to grade imperceptibly (via intermediate morphologies) to the essentially uniform toothrows of other taxa (e.g., *Lestodelphys* and *Marmosa canescens*, in which I2 and I5 are subequal) without obvious discontinuities to permit qualitative coding.

An alternative morphology in which the crowns of I2–I5 are conspicuously asymmetrical, with much longer anterior (mesial) than posterior (distal) cutting edges, occurs in *Caluromys*, *Caluromysiops*, *Didelphis*, *Glironia*, *Lutreolina*, and *Philander*. On unworn teeth of these taxa, the anterior angle (mesiostyle) is more frequently distinct than is the posterior angle (distostyle), which is often entirely lacking on I5 (fig. 11B). This is the morphology that Takahashi (1974) labeled "incisiform", which she recorded for *Chironectes* in addition to *Caluromys*, *Didelphis*, *Lutreolina*, and *Philander* in her study. However, the unworn juvenile dentitions of *Chironectes* that we examined (e.g., AMNH 126979, 127563, 264573) have approximately symmetrical, rhomboidal crowns. There is a ten-

[9] An alternative hypothesis of marsupial dental homologies interprets the replaced tooth as M1/m1 (after Archer, 1978) and numbers the premolars on the assumption that P2/p2 is missing (after Thomas, 1887). According to this system (which was followed inter alia by Creighton [1984], Reig et al. [1987], and Hershkovitz [1992b]), the seven postcanine teeth of adult didelphids are P1/p1, P3/p3, P4/p4, M2/m2, M3/m3, M4/m4, and M5/m5.

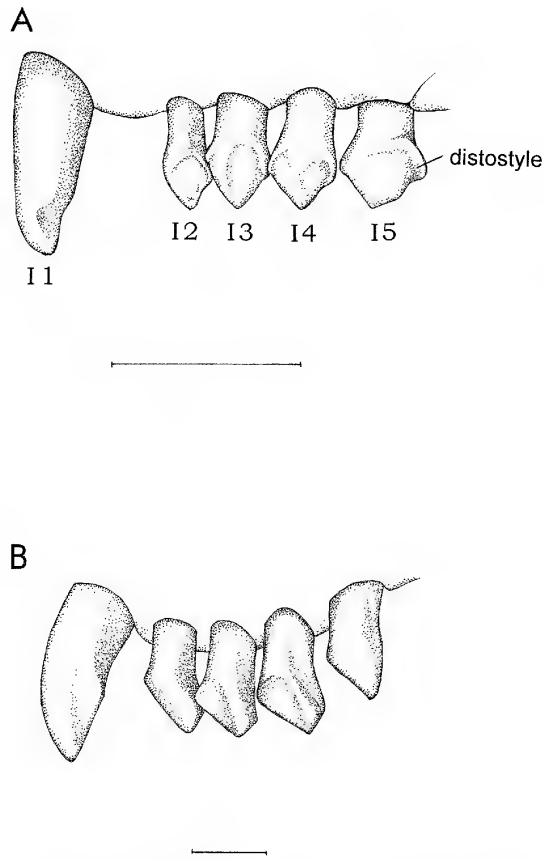


Fig. 11. Unworn premaxillary dentitions of *Marmosops pinheiroi* (**A,** AMNH 267341) and *Lutreolina crassicaudata* (**B,** AMNH 210422) illustrating taxonomic differences in the shape of the incisor crowns. In *Marmosops* and many other small didelphines, the crowns of I2–I5 are symmetrically rhomboidal, with subequal anterior (mesial) and posterior (distal) cutting edges that converge to form a sharp central apex; a distinct posterior corner (distostyle) is always present on I5. By contrast, in *Lutreolina* (and certain other taxa), the crowns of I2–I5 are conspicuously asymmetrical, with longer anterior than posterior cutting edges; a distinct distostyle is usually absent on I5. Scale bars = 1 mm.

dency (more marked in *Glironia* than in other genera of this category) for I2–I5 to decrease in breadth from front to back, such that I2 is sometimes visibly larger than I5 in labial view.

Some published descriptions of didelphid incisor morphology are impossible to reconcile with our observations. Archer (1976b: character 3), for example, coded the upper incisor crowns of *Marmosa* as "spatulate" versus the presumably nonspatulate condition that he recorded for other didelphids in his data matrix (e.g., *Didelphis*, *Metachirus*, and *Philander*). Subsequently, Kirsch and Archer (1982: character 2) coded the upper incisors of *Caluromys*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Marmosa*, and *Philander* as "round" versus the "spatulate" condition they observed in *Chironectes*, *Glironia*, *Monodelphis*, and *Metachirus*. Unfortunately, no definitions of these ambiguous and apparently contradictory descriptors were provided, and we have not been able to discover any aspect of incisor shape that corresponds to the pattern of taxonomic scoring in either study.

Character 53: *Upper canine simple, without distinct accessory cusps (0); or with distinct posterior accessory cusp (1); or with anterior and posterior accessory cusps (2).* Although the upper canine (C1) is a simple unicuspid tooth in most didelphids, some species (e.g., *Marmosa lepida*) have a small but distinct posterior accessory cusp, and others (e.g., *Marmosops parvidens* and *M. pinheiroi*; see Voss et al. 2001: fig. 26) have both anterior and posterior accessory cusps. Some care is needed in scoring this character because posterior accessory cusps are sometimes obliterated by attrition (as inferred from their absence in old adults of species that uniformly exhibit such structures as juveniles and subadults). Alternatively, a false accessory cusp is sometimes formed when the posterior edge of C1 is notched by occlusion with p1. Therefore, confident scoring of this character should be based on unworn dentitions. Because no didelphid known to us has an anterior cusp without having a posterior cusp, state 1 appears to represent an intermediate condition in the premolarization of C1. We therefore treated this character as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) in all of our analyses.

Because taxa with distinct accessory cusps on C1 also have distinct accessory cusps on c1 (which is likewise premolarized), we did not score the latter as an independent character.

Character 54: *First upper premolar (P1) large, at least one-half the height or width of P2 (0); or vestigial, less than one-third the height or width of P2, or absent (1).* Most didelphids have a relatively large first max-

illary premolar (as operationally defined above) that essentially resembles P2 and P3 in having a well-defined central cusp flanked by anterior and posterior cutting edges that persist as recognizable occlusal features into adult life. In *Caluromys* and *Caluromysiops*, however, P1 is relatively much smaller and lacks prominent occlusal features, usually persisting into adulthood (if at all) as a simple peglike structure; P1 is bilaterally absent in some specimens of *Caluromysiops* (e.g., AMNH 244364). *Glironia* exhibits an apparently intermediate morphology, but more closely resembles the common didelphid condition (state 0), a similarity that we scored as such rather than create a unique code for this taxon. Although Reig et al. (1987: character 22) recorded the same taxonomic pattern of variation that we observed for this character, Kirsch and Archer (1982: character 44) did not. Unfortunately, the lack of explicit scoring criteria in previous phylogenetic analyses precludes any substantive evaluation of such discrepancies.

Character 55: *P2 distinctly taller than P3 (0); or P2 and P3 subequal in height (1); or P3 distinctly taller than P2 (2).* Didelphid variation in the relative sizes of P3 and P2 was first scored for phylogenetic analysis by Kirsch and Archer (1982: character 4), who recognized only two states ("P3 greater than P2" versus "P3 less than P2"). Scoring by this criterion, however, is problematic for taxa in which these teeth are subequal, and size differences are hard to assess without explicit reference to dental dimensions. Reig et al. (1987: character 23) scored P3 as either "longer" or "shorter" than P2, but crown height is a more convenient criterion for visual comparisons (Wroe, 1997; Wroe et al., 2000).

Among the taxa included in this analysis, P2 is distinctly taller than P3 only in *Caluromys* and *Caluromysiops*. P3 is distinctly the taller tooth in *Chironectes*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Monodelphis*, *Philander*, and *Thylamys*. P2 and P3 are subequal in the remaining didelphids examined in this study. Because state 1 is clearly intermediate to the others, we treated this character as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 56: *P3 with well-developed anterior and posterior cutting edges (0); or only posterior cutting edge well developed (1).* The unworn upper third premolar is provided with sharp anterior and posterior cutting edges, each of which extends from the cingulum to the apex of the tooth, in *Caluromys*, *Caluromysiops*, and *Glironia*. In all of the remaining didelphids we examined, however, the anterior margin of the tooth is rounded, and only the posterior cutting edge is well developed. Small anterior blades are variably present near the base of P3 in *Chironectes* and *Philander*, but the apex of the tooth is always rounded anteriorly as in the other taxa that we code with state 1.

Other workers have remarked marsupial variation in P3, distinguishing "inflated" or "bulbous" teeth on the one hand from "laterally compressed", "bladelike", or "normal" teeth on the other, but we are unable to recognize these descriptors as distinct alternatives among the taxa included in our analysis. Contradictory coding for P3 morphology in different studies (e.g., *Didelphis*, scored as "bulbous" by Reig et al. [1987: character 24], but as "laterally compressed" by Wroe et al. [2000: character 6]) clearly indicates the ambiguity of such undefined contrasts. Well-developed anterior cutting edges occur on taxa with "bulbous" P3s (e.g., *Caluromysiops*) and with "normal" teeth (e.g., *Glironia*) according to Reig et al.'s (1987) scoring of premolar shape variation.

Character 57: *First upper molar (M1) wider than M4, the molar dentition as a whole not or weakly carnassialized (0); or M4 wider than M1, the molar dentition moderately to strongly carnassialized (1).* Didelphid molar dentitions differ conspicuously in the relative width (transverse or labial-lingual dimension) of teeth within toothrows. In *Caluromys* and *Caluromysiops* the anterior molars are wide in proportion to more posterior teeth, but the posterior teeth are much wider in other didelphids. Our visual comparisons of toothrows suggest that these proportional differences are correlated with a complex pattern of molar transformation that has previously been described in the literature as "carnassialization" (Reig and Simpson, 1972: 534) or as "an emphasis on post-

vallum-prevalid shear" (Muizon and Lange-Badré, 1997).

Tribosphenic molar occlusion results in shearing forces created by the relative movement of opposing edges on the upper molar trigons and the lower molar trigonids, together with the crushing action of the protocone as it penetrates the talonid basin. Because adjacent marsupial molars are not separated from one another by diastemas, and because upper and lower teeth interlock tightly in occlusion, enlargement or reduction of one dental structure necessarily involves reciprocal changes in other parts. As described by numerous authors (e.g., Reig and Simpson, 1972; Reig et al., 1987; Muizon and Lange-Badré, 1997), the shearing (carnassial) action of marsupial molars is emphasized in taxa with large metacristae (on the posterior wall or vallum of the trigon, hence "postvallum") that occlude with large paracristids (on the anterior wall of the trigonid, hence "prevallid"); the same taxa also tend to have relatively small paracones, protocones, metaconids, and talonids. These tendencies are redundantly described by numerous dental ratios that have been coded as independent characters in previous phylogenetic studies (see appendix 4).

We measured molar widths (from the stylar shelf at or near the "A" position to the lingual surface of the protocone) in order to document the proportional differences we observed involving the most anterior and posterior elements of the toothrow, and we measured the lengths of the metacrista and postprotocrista of M3 to obtain an index of carnassialization.[10] A bivariate plot of these data (fig. 12) effectively illustrates the divergence of *Caluromys* and *Caluromysiops* from other didelphids in both respects, and the essentially continuous variation that precludes recognition of additional states (despite a wide range of morphologies) among members of the latter group.

Character 58: *Centrocrista of M1–M3 linear, its apex almost level with the floor of the trigon basin (0); or weakly V-shaped, its apex distinctly elevated above the trigon basin (1); or strongly V-shaped, its apex high above the trigon basin (2).* The shape of the centrocrista (postparacrista + premetacrista) and the descriptive nomenclature associated with its alternative states have been a source of some confusion among marsupial researchers. Traditionally, taxa with a V-shaped (labially inflected) centrocrista have been described as "dilambdodont" because the ectoloph (preparacrista + centrocrista + postmetacrista) is then W-shaped (like two inverted lambdas), whereas taxa with a straight (uninflected) centrocrista have usually been called "predilambdodont" (e.g., by Reig et al., 1987). Unfortunately, neither descriptor applies unambiguously to some didelphids (Goin, 1997), and certain taxa have been coded with contradictory character states in different phylogenetic datasets. *Didelphis*, for example, was coded as having a V-shaped centrocrista by Reig et al. (1987: character 1) and Wible et al. (2001: character 31), but Wroe et al. (2000: character 10) scored it as having a linear centrocrista. Our coding reflects Johanson's (1996) observation that the shape (linearity versus labial inflection) of this crest is correlated with its occlusal relief (apical height above the trigon basin), and we recognize an intermediate condition for taxa that do not conform with either traditionally recognized morphotype.

Among the taxa included in our study, only *Caluromysiops* has a truly linear centrocrista on M1–M3. In this taxon, the apex of the centrocrista is essentially level with the floor of the trigon basin, clearly conforming to the predilambdodont condition defined by Johanson (1996). By contrast, the centrocrista is strongly inflected labially (buccally)—and therefore distinctly V-shaped—in *Gracilinanus*, *Lestodelphys*, *Marmosa*, *Marmosops*, *Metachirus*, *Micoureus*, *Monodelphis*, and *Thylamys*; the apex of the crest is ele-

[10] Of the many dental structures affected by carnassialization, the metacrista is the easiest to measure, and its hypertrophy relative to the postprotocrista (see fig. 12) is conveniently indexed by the ratio of their lengths, which we measured on M3. By contrast, cusp heights are more sensitive to intraspecific differences in toothwear, and other dental structures (such as lengths of the talonid and trigonid) are hard to measure repeatably.

Metacrista length (MCL) was measured from the apex of the metacone to stylar position E, and postprotocrista length (PCL) was measured from the apex of the protocone to the base of the metacone. We tried to measure these dimensions on minimally worn teeth of five specimens per species, but this was not always possible. The ratio MCL/PCL was computed from the species means for both measurements.

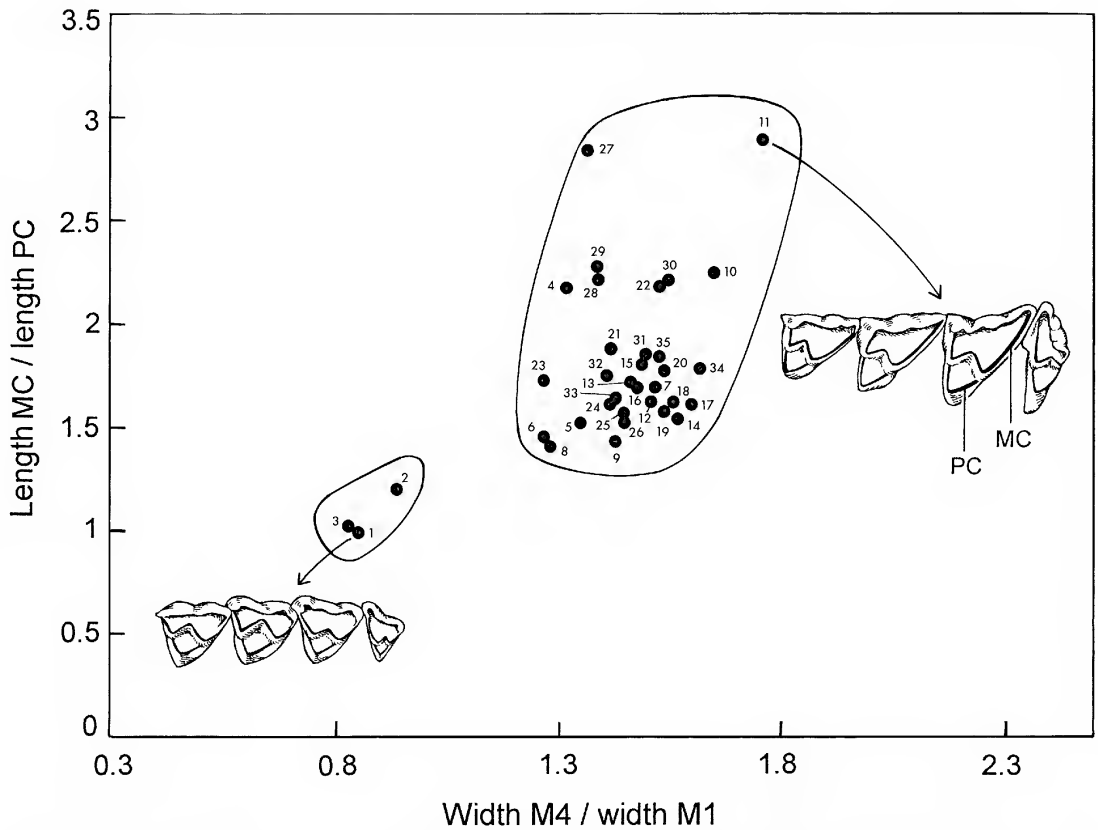


Fig. 12. Bivariate comparison of two dental proportions discussed in the text, with illustrated examples of contrasting morphologies. Closed curves delimit sets of taxa assigned to alternative states of character 57. Taxon labels: **1,** *Caluromys lanatus*; **2,** *Caluromys philander*; **3,** *Caluromysiops irrupta*; **4,** *Chironectes minimus*; **5,** *Didelphis albiventris*; **6,** *Didelphis marsupialis*; **7,** *Didelphis virginiana*; **8,** *Glironia venusta*; **9,** *Gracilinanus microtarsus*; **10,** *Lestodelphys halli*; **11,** *Lutreolina crassicaudata*; **12,** *Marmosa canescens*; **13,** *Marmosa lepida*; **14,** *Marmosa mexicana*; **15,** *Marmosa murina*; **16,** *Marmosa robinsoni*; **17,** *Marmosa rubra*; **18,** *Marmosops impavidus*; **19,** *Marmosops incanus*; **20,** *Marmosops noctivagus*; **21,** *Marmosops parvidens*; **22,** *Marmosops pinheiroi*; **23,** *Metachirus nudicaudatus*; **24,** *Micoureus demerarae*; **25,** *Micoureus paraguayanus*; **26,** *Micoureus regina*; **27,** *Monodelphis adusta*; **28,** *Monodelphis brevicaudata*; **29,** *Monodelphis emiliae*; **30,** *Monodelphis theresa*; **31,** *Philander frenata*; **32,** *Philander mcilhennyi*; **33,** *Philander opossum*; **34,** *Thylamys pallidior*; **35,** *Thylamys venustus*. Other labels: **MC,** metacrista; **PC,** postprotocrista.

vated well above the trigon floor in these taxa, which are unambiguously dilambdodont sensu Johanson (1996). The intermediate condition occurs in the six remaining genera (*Caluromys*, *Chironectes*, *Didelphis*, *Glironia*, *Lutreolina*, *Philander*) in which the centrocrista has a weak labial inflection with a slightly elevated apex; these taxa could appropriately be described as weakly dilambdodont. Because these states appear to represent successive stages in a single complex transformation of occlusal architecture with the weakly dilambdodont condition intermediate to the others, we treated this character as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 59: *Upper molars without a distinct ectoflexus on any tooth (0); or distinct ectoflexus present on one or more teeth (1).* Among the taxa examined for this analysis, only *Caluromys* and *Caluromysiops* lack any trace of an ectoflexus on the upper molars. A distinct ectoflexus is present on M3, on M2 and M3, or (rarely) on M1–M3

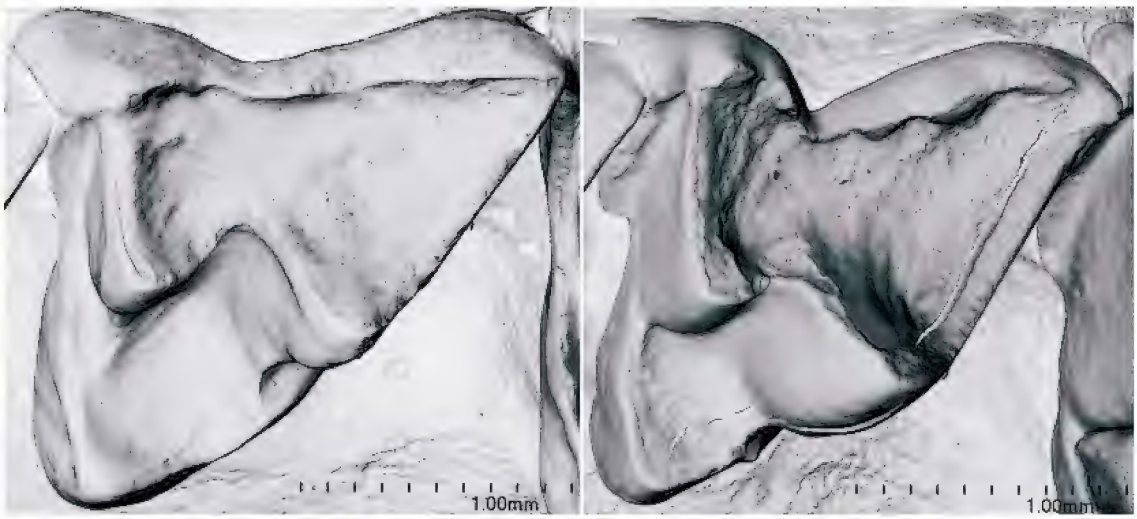


Fig. 13. Anterolingual views of left M3 illustrating taxonomic differences in cingular morphology. **Left,** *Marmosa murina* (AMNH 272870) with preprotocrista and anterolabial cingulum joined to form a continuous shelf along the anterior margin of the tooth crown. **Right,** *Monodelphis adusta* (AMNH 272781) with separate crista and cingulum (no continuous shelf).

in all other didelphids. Rougier et al. (1998: character 19) scored the presence or absence of a "deep" ectoflexus on M2 and M3, but a complete range of intermediate conditions of the ectoflexus from shallow to deep among the taxa treated herein precludes unambiguous scoring of such distinctions.

Character 60: *Preprotocrista and anterolabial cingulum joined to form a continuous shelf along the anterior margin of M3 (0); or crista and cingulum separate, not forming a continuous shelf (1).* In many didelphids (*Caluromys*, *Caluromysiops*, *Glironia*, *Gracilinanus*, *Marmosa*, *Marmosops parvidens*, *Micoureus*) the preprotocrista passes labially around the base of the paracone to join with the anterolabial cingulum, forming a continuous shelf along the anterior margin of the crown of each of the first three maxillary molars (fig. 13, left). In the alternative morphology exhibited by *Chironectes*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Marmosops* (except *M. parvidens*), *Metachirus*, *Monodelphis*, *Philander*, and *Thylamys*, the preprotocrista extends only to a point at or near the base of the paracone; the anterolabial cingulum does not converge toward the preprotocrista in these taxa, but passes obliquely dorsally such that the two crests are discontinuous on the anterior surface of the tooth crown (fig. 13, right). Because this occlusal feature sometimes varies along the toothrow, we standardized our taxonomic scoring by recording the condition observed on M3.

Archer (1976b: characters 31, 32), Creighton (1984: character 53), and Wroe et al. (2000: character 25) referred to state 0 as comprising a "complete" anterior cingulum, and state 1 as an "incomplete or absent" cingulum. However, whereas Creighton and Wroe et al. reported essentially the same taxonomic variation that we observed, Archer recorded the presence of a complete cingulum in *Philander opossum*, a species (and genus) that uniformly lacks this feature in our material. Similarly, Rougier et al. (1998) and Wible et al (2001: character 33) scored the preprotocrista of *Didelphis* as extending labially beyond the base of the paracone, an apparent lapsus; in all specimens of *Didelphis* that we examined, the preprotocrista terminates at the base of the paracone with no trace of a labial extension.

Character 61: *Fourth upper molar erupts before P3 (0); or M4 and P3 erupt simultaneously (1); or P3 erupts before M4 (1).* As described by Tribe (1990), M4 is the penultimate upper tooth to erupt in most didelphids, followed by P3; by contrast, P3 erupts before M4 in *Chironectes*, *Didelphis*, *Lutreo-*

lina, and *Philander*. We also coded an intermediate condition for taxa in which M4 and P3 erupt simultaneously (*Metachirus nudicaudatus*, *Monodelphis brevicaudata*) and treated this character as ordered (0 ↔ 1 ↔ 2) in all of our analyses. Suitable subadult material was not available to determine eruption sequences for several species (*Micoureus paraguayanus*, *Monodelphis emiliae*, *M. theresa*, *Philander frenata*), which are scored as missing ("?") in our data matrix.

Character 62: *Distinct lingual cusp of lower incisors present (0); or absent (1).* The unworn lower incisors of most didelphids have a distinct lingual (posterior) cusp or heel (fig. 14, top) that is entirely lacking in *Chironectes*, *Didelphis*, *Lutreolina* (fig. 14, bottom), and *Philander*. This character has the same taxonomic distribution among didelphids as Takahashi's (1974) distinction between the "subrectangular" teeth of *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* on the one hand, and the "suboval" lower incisors of *Caluromys*, *Marmosa*, *Metachirus*, and *Monodelphis* on the other, but we are unable to appreciate the basis for her shape descriptors.

Character 63: *Second lower premolar distinctly taller than p3 (0); or p2 and p3 subequal in height (1); or p3 distinctly taller than p2 (2).* The second lower premolar is distinctly taller than p3 in most didelphids, but p2 and p3 are subequal in *Thylamys* and in most species of *Monodelphis*. In *Lestodelphys* and *Monodelphis emiliae*, however, p3 is distinctly taller than p2. Due to the obviously intermediate condition represented by state 1, this character was treated as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 64: *Deciduous lower third premolar (dp3) with distinctly tricuspid (complete) trigonid (0); or with unicuspid or bicuspid (incomplete) trigonid (1).* Although most previous descriptions of didelphid milk teeth have described them as large and molariform (Flower, 1867; Thomas, 1888; Bensley, 1903; Tate, 1948; Archer, 1976b), taxonomically significant variation in the size and shape of dp3 was reported by Voss et al. (2001: table 5). Many didelphids (*Caluromys lanatus*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, *Marmosops*, *Metachirus*, *Monodelphis emiliae*, *Philander*) have a fully molariform dp3 in which the trigonid is represented by its normal complement of three cusps (paraconid, protoconid, metaconid) in a more-or-less triangular configuration (fig. 15, top). A fully molariform dp3 is also the modal condition for *Monodelphis brevicaudata*, in which seven of nine specimens examined with intact milk dentitions had complete trigonids. By contrast, dp3 is only partially molariform in *Lestodelphys*, *Marmosa*, *Micoureus*, and *Thylamys*, which have incomplete, blade-like trigonids bearing only one or two distinct cusps (fig. 15, bottom). Scoring *Caluromys philander* for this character was somewhat problematic because only the protoconid of dp3 is usually distinct in our material, but the trigonid is triangular in outline and more closely resembles the fully molariform condition than the blade-like bicuspid alternative. We did not examine juvenile specimens of several taxa (*Glironia*, *Gracilinanus*, *Marmosops incanus*, *Micoureus paraguayanus*, *Monodelphis adusta*, *M. theresa*, and *Philander frenata*) that are scored as missing ("?") in our matrix.

Character 65: *Lower third molar hypoconid labially salient (0); or m3 hypoconid lingual to salient protoconid (1).* The hypoconid of m3 is labially salient (projecting beyond the protoconid, or level with it) in most didelphids, but the hypoconid is lingual to the protoconid on m3 in *Lestodelphys* and *Monodelphis*. Goin and Rey (1997: character 20) described the hypoconids of *Monodelphis* as "poco salientes labialmente" versus the alternative condition of "[h]ipocónidos salientes labialmente" attributed to the tribe Marmosini (including *Lestodelphys*), an observation that conflicts with our assessment, but for which we can offer no explanation.

Character 66: *Entoconid large and well developed on m1–m3 (0); or very small or indistinct (1).* Most didelphids have a well-developed entoconid that is about as tall as the hypoconid and much exceeds the adjacent hypoconulid in height and breadth on m1–m3 (fig. 16, top). In *Monodelphis*, however, the entoconid is very small, never more than subequal to the hypoconulid, and often smaller than that cusp (fig. 16, bottom); it becomes indistinct or is obliterated by wear in most adult specimens. Our scoring of didelphid entoconid variation differs only in

Fig. 14. Lingual views of anterior mandibular dentition illustrating taxonomic differences in lower incisor morphology. **Top,** *Metachirus nudicaudatus* (AMNH 266452) with distinct posterior accessory cusps on i1–i4. **Bottom,** *Lutreolina crassicaudata* (AMNH 210424) without distinct posterior accessory cusps on i1–i5.

minor details from coding schemes previously suggested by Archer (1976b: character 43), Creighton (1984: character 58), Goin and Rey (1997: character 21), Rougier et al. (1998: character 54), and Wroe et al. (2001: character 41), chiefly by discounting cusp shape (as too subjective to categorize) and by not distinguishing cusp reduction from

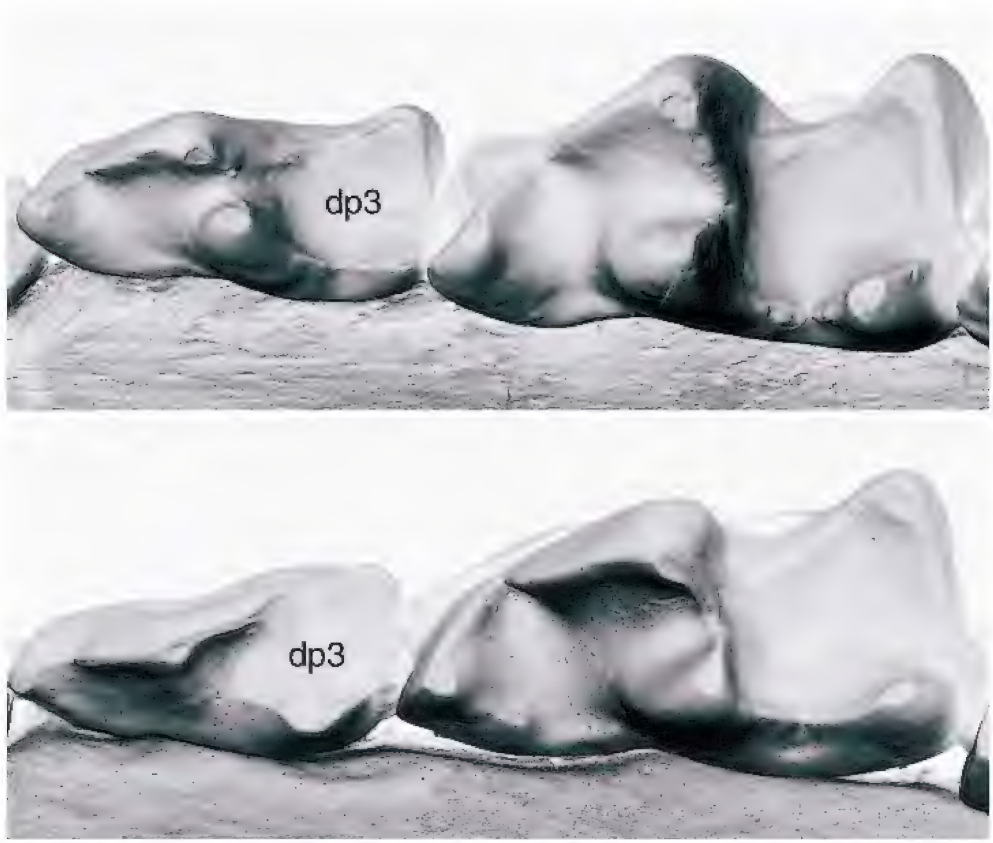


Fig. 15. Occlusal views of right dp3 and m1 illustrating taxonomic differences in trigonid morphology of the deciduous tooth. **Top,** *Marmosa murina* (MUSM 15297) with a distinctly tricuspid (complete) dp3 trigonid. **Bottom,** *Marmosops impavidus* (MUSM 13286) with a bicuspid (incomplete) dp3 trigonid.

absence (an entoconid could be distinguished in all examined specimens with newly erupted teeth). Kirsch and Archer (1982: character 17) coded *Lestodelphys* as having a small entoconid like that of *Monodelphis*, but our material of *Lestodelphys* (especially specimens with newly erupted teeth; e.g., MMNH 17171) more closely resembles the entoconid morphology that we observed in other didelphids.

Character 67: *Hypoconulid at posterolingual margin of talonid, "twinned" with entoconid on m1–m3 (0); or at midline of tooth, approximately equidistant to hypoconid and entoconid, not "twinned" with the latter cusp (1).* Among didelphids, only *Caluromysiops* has a hypoconulid that is not "twinned" with the entoconid, but this trait is widespread among placentals and basal therians (see data matrices in Cifelli, 1993; Wible et al., 2001). We scored this character on the first three lower molars because the entoconid is sometimes missing from m4.

Karyotypes

An extensive literature on marsupial chromosomes (reviewed by Sharman, 1973; Hayman, 1977, 1990; and Reig et al., 1977) documents taxonomic variation in diploid numbers, pericentric inversions, heterochromatin distribution, sex chromosome morphology, and other cytogenetic traits. Despite this wealth of comparative data, only differences in diploid numbers are currently tractable for phylogenetic analysis. Easily determined from Giemsa-stained preparations of field-collected bone-marrow cells, diploid counts

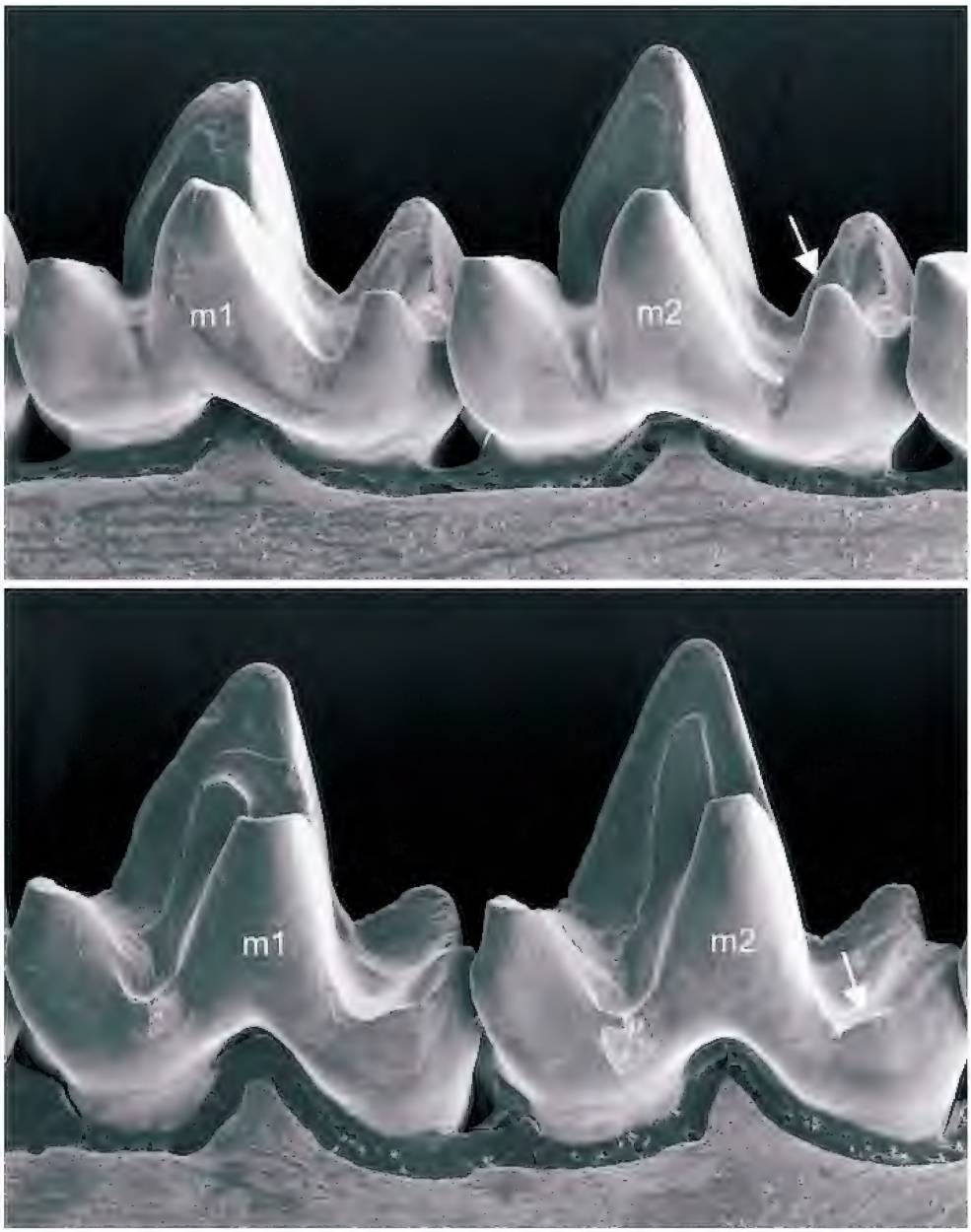


Fig. 16. Lingual views of right m2 and m3 illustrating taxonomic differences in entoconid size. **Top,** *Thylamys pallidior* (AMNH 262405) with a large entoconid (arrow). **Bottom,** *Monodelphis adusta* (AMNH 272781) with an indistinct entoconid (arrow).

are available for the majority (77%) of the taxa included in this study and appear to be invariant within all sampled species. By contrast, some chromosomal traits cannot be scored without special preparations (e.g., to determine NOR-banding) that are unavailable for most taxa, and other characters are prone to subjective and inconsistent scoring (e.g., morphology of the sex chromosomes), as indicated by divergent interpretations of the same material by different investigators.

Most marsupials have a diploid number ($2n$) of 14 chromosomes, and this is also the most widespread number among the didel-

phids included in our study (table 2). By contrast, all karyotyped species of *Monodelphis* have diploid counts of 18 chromosomes, whereas complements of $2n = 22$ have been reported from *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*, and *Marmosa canescens*. Morphometric comparisons and G-banding studies indicate that each of these diploid groupings are homogeneous in the sense that different taxa with the same diploid number have chromosomes with essentially similar relative sizes, shapes (arm ratios), and banding patterns (Reig et al., 1977; Rofe and Hayman, 1985; Svartman and Vianna-Morgante, 1999). By implication, a shared history of Robertsonian changes (centric fissions or centric fusions) could account for the taxonomic membership of each diploid category.

A minimum of four centric fission/fusion events is required to account for the difference in diploid number between karyotypes with 14 chromosomes and those with 22 chromosomes. Based on arm homologies suggested by G-banding patterns, the following Robertsonian transformations involving eight acrocentric (acr) autosomes in the $2n = 22$ karyotype and four metacentric (met) autosomes in the $2n = 14$ karyotype are indicated (chromosomes are numbered from small to large within each karyotype): acr1 + acr5 ↔ met1, acr2 + acr8 ↔ met2, acr3 + acr10 ↔ met3, and acr6 + acr9 ↔ met4 (Svartman and Vianna-Morgante, 1999). The $2n = 18$ karyotype is intermediate because it has only two metacentric autosomes, of which the larger can be homologized with acr2 + acr8 of the $2n = 22$ karyotype and with met2 of the $2n = 14$ karyotype, whereas the smaller metacentric can be homologized with acr6 + acr9 of the $2n = 22$ karyotype and with met4 of the $2n = 14$ karyotype (op. cit.).

Although Creighton (1984: character 39) and Reig et al. (1987: character 36) coded didelphid karyotypic variation as a single character with different diploid numbers (14, 18, and 22) as alternative states, the transformational homologies suggested by G-banding patterns are more appropriately coded as separate characters, one for each set of Robertsonian equivalents—for example, {acr2 + acr8, met2}—which can exist in two states: fused (metacentric) or fissioned (acrocentric). Two character-state changes would then distinguish taxa with $2n = 14$ from those with $2n = 18$, and two additional changes would separate taxa with $2n = 18$ from those with $2n = 22$. (Note that, in applications of data resampling procedures, treating each Robertsonian transformation as a different character is not computationally equivalent to weighting each transformation of the series 14 ↔ 18 ↔ 22 by a factor of two.) The crucial issue here is the independence or nonindependence of different fission/fusion events. Perhaps the most persuasive argument for nonindependence is that there are no known didelphids with $2n = 16$ or $2n = 20$ chromosomes, but such complements are clearly not impossible because they have been reported from various Australasian marsupials (Hayman, 1990: table 1).

Character 68: *Robertsonian equivalents {acr1 + acr5, met1} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

Character 69: *Robertsonian equivalents {acr2 + acr8, met2} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

Character 70: *Robertsonian equivalents {acr3 + acr10, met3} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

Character 71: *Robertsonian equivalents {acr6 + acr9, met4} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

Dataset Summary and Analytic Results

The dataset described above includes 28 characters based on external morphology, 23 characters of the skull and mandible, 16 dental characters, and 4 karyotypic characters. Sixty-six characters (93% of the total) are parsimony-informative, and the remaining 5 (7%) are autapomorphic. Fifty-four characters (76%) are binary, 11 (15%) describe ordered multistate (additive) transformation, and 6 (8%) describe unordered multistate (nonadditive) transformations. The data matrix (appendix 5) has $71 \times 35 = 2485$ cells, of which only 65 (3%) are scored as missing ("?") and 29 (1%) are scored as inapplicable

TABLE 2
Sources of Didelphid Karyotypic Data

Taxon	$2n$[a]	References[b,c]
Caluromys lanatus	14	Reig et al. (1977), Palma and Yates (1996), Patton et al. (2000)
Caluromys philander	14	Reig et al. (1977)
Chironectes minimus	22	Reig et al. (1977), Palma and Yates (1996)
Didelphis albiventris	22	Reig et al. (1977), Palma and Yates (1996)
Didelphis marsupialis	22	Gardner (1973), Reig et al. (1977), Palma and Yates (1996), Patton et al. (2000)
Didelphis virginiana	22	Gardner (1973), Reig et al. (1977)
Gracilinanus microtarsus	14	Wainberg et al. (1979), Carvalho et al. (2002)
Lestodelphys halli	14	Birney et al. (1996)
Lutreolina crassicaudata	22	Reig et al. (1977), Palma and Yates (1996)
Marmosa canescens	22	Engstrom and Gardner (1988)
Marmosa mexicana	14	Biggers et al. (1965)
Marmosa murina	14	Reig et al. (1977)
Marmosa robinsoni	14	Reig et al. (1977)
Marmosops impavidus	14	Patton et al. (2000)
Marmosops incanus	14	Carvalho et al. (2002)
Marmosops noctivagus	14	Palma and Yates (1996), Patton et al. (2000)
Metachirus nudicaudatus	14	Reig et al. (1977), Palma and Yates (1996), Patton et al. (2000)
Micoureus demerarae[d]	14	Reig et al. (1977), Palma and Yates (1996), Patton et al (2000)
Micoureus paraguayanus[e]	14	Carvalho et al. (2002)
Micoureus regina	14	Patton et al. (2000)
Monodelphis brevicaudata[f]	18	Carvalho et al. (2002)
Monodelphis emiliae	18	Patton et al. (2000)
Philander frenata	22	Carvalho et al. (2002)
Philander mcilhennyi	22	Reig et al. (1977), Patton et al. (2000)
Philander opossum	22	Reig et al. (1977)
Thylamys pallidior	14	Palma and Yates (1996)
Thylamys venustus[g]	14	Palma and Yates (1996)

[a]Diploid number.

[b]Listed references are those we consulted for information about diploid number. This is not an exhaustive catalog of karyotypic data for these taxa.

[c]Karyotyped specimens identified as *Marmosops parvidens* by Palma and Yates (1996) and Carvalho et al. (2002) are probably referable to other taxa. *Marmosops parvidens* sensu stricto is largely restricted to northeastern Amazonia (Voss et al., 2001).

[d]Identified as *Marmosa cinerea* by Reig et al. (1977), and as *Micoureus cinereus* by Palma and Yates (1996).

[e]The *Micoureus demerarae*-like specimens that Carvalho et al. (2002) karyotyped from Rio Grande do Sul are referrable to this taxon (see appendix 3).

[f]Some karyotyped specimens previously identified in the literature as *Monodelphis brevicaudata* (sensu lato) probably represent other closely related species of the *brevicaudata* complex. Based on known geographic ranges (summarized by Voss et al., 2001), the northern Venezuelan material reported as *M. brevicaudata* by Reig et al. (1977) is referable to *M. palliolata*, whereas the Bolivian material reported as *M. brevicaudata* by Palma and Yates (1996) is referable to *M. glirina*.

[g]Karyotyped Bolivian material identified as *Thylamys elegans* by Palma and Yates (1996) was reidentified as *T. venustus* by Palma and Yates (1998).

("-"). The remaining 2391 matrix cells (96%) record organismal attributes, with data completeness for individual terminal taxa ranging from 83 to 100% (table 3).

A heuristic analysis of these data recovered 2161 equally most-parsimonious trees, each of which is consistent with our assumption of ingroup (didelphine) monophyly. Among the four caluromyine taxa available for rooting to compute the strict consensus (fig. 17) we chose *Glironia* for consistency with the results of our previous molecular study (Jansa and Voss, 2000), which included nondidelphid outgroups. The other three caluromyines then form a single clade, within which *Caluromysiops irrupta* is the sister group of *Caluromys lanatus* + *C. philander*.

Unfortunately, the deep branching struc-

TABLE 3
Nonmolecular Data Completeness for Didelphid Terminal Taxa

	Matrix cells scored as		
	Missing	Inapplicable	% complete[a]
Caluromys lanatus	0	0	100
Caluromys philander	0	0	100
Caluromysiops irrupta	5	1	92
Chironectes minimus	0	0	100
Didelphis albiventris	0	0	100
Didelphis marsupialis	0	0	100
Didelphis virginiana	0	0	100
Glironia venusta	10	2	83
Gracilinanus microtarsus	3	1	94
Lestodelphys halli	1	1	97
Lutreolina crassicaudata	0	1	99
Marmosa canescens	0	1	99
Marmosa lepida	4	1	93
Marmosa mexicana	0	1	99
Marmosa murina	0	1	99
Marmosa robinsoni	0	1	99
Marmosa rubra	6	1	90
Marmosops impavidus	0	1	99
Marmosops incanus	2	1	96
Marmosops noctivagus	0	1	99
Marmosops parvidens	4	1	93
Marmosops pinheiroi	4	1	93
Metachirus nudicaudatus	0	1	99
Micoureus demerarae	0	1	99
Micoureus paraguayanus	3	1	94
Micoureus regina	0	1	99
Monodelphis adusta	5	2	90
Monodelphis brevicaudata	0	2	97
Monodelphis emiliae	1	2	96
Monodelphis theresa	9	2	85
Philander frenata	2	0	97
Philander mcilhennyi	0	0	100
Philander opossum	0	0	100
Thylamys pallidior	3	0	96
Thylamys venustus	3	0	96

[a] Calculated as $100n/71$, where n represents the number of filled cells for each species in our nonmolecular data matrix (appendix 5).

ture of didelphine phylogeny is not well resolved by nonmolecular characters. Instead, four species of *Marmosa* and three species of *Micoureus* participate in a large basal polytomy, and two additional species of *Marmosa* form a second polytomy with other didelphines at the next-highest node. Because most included species of *Marmosa* and *Micoureus* can be distinguished from one another by parsimony-informative nonmolecular characters (only *Micoureus demerarae* and *M. regina* are not), this bushy structure principally results from character conflict rather than lack of data.

Gracilinanus (represented only by *G. microtarsus* in this analysis) appears as the sister group to the remaining didelphines, of which the next branch is a monophyletic cluster of five species of *Marmosops*. Within the latter genus, *M. incanus* and *M. noctivagus* form an unresolved polytomy with a group that includes *M. impavidus* and the sis-

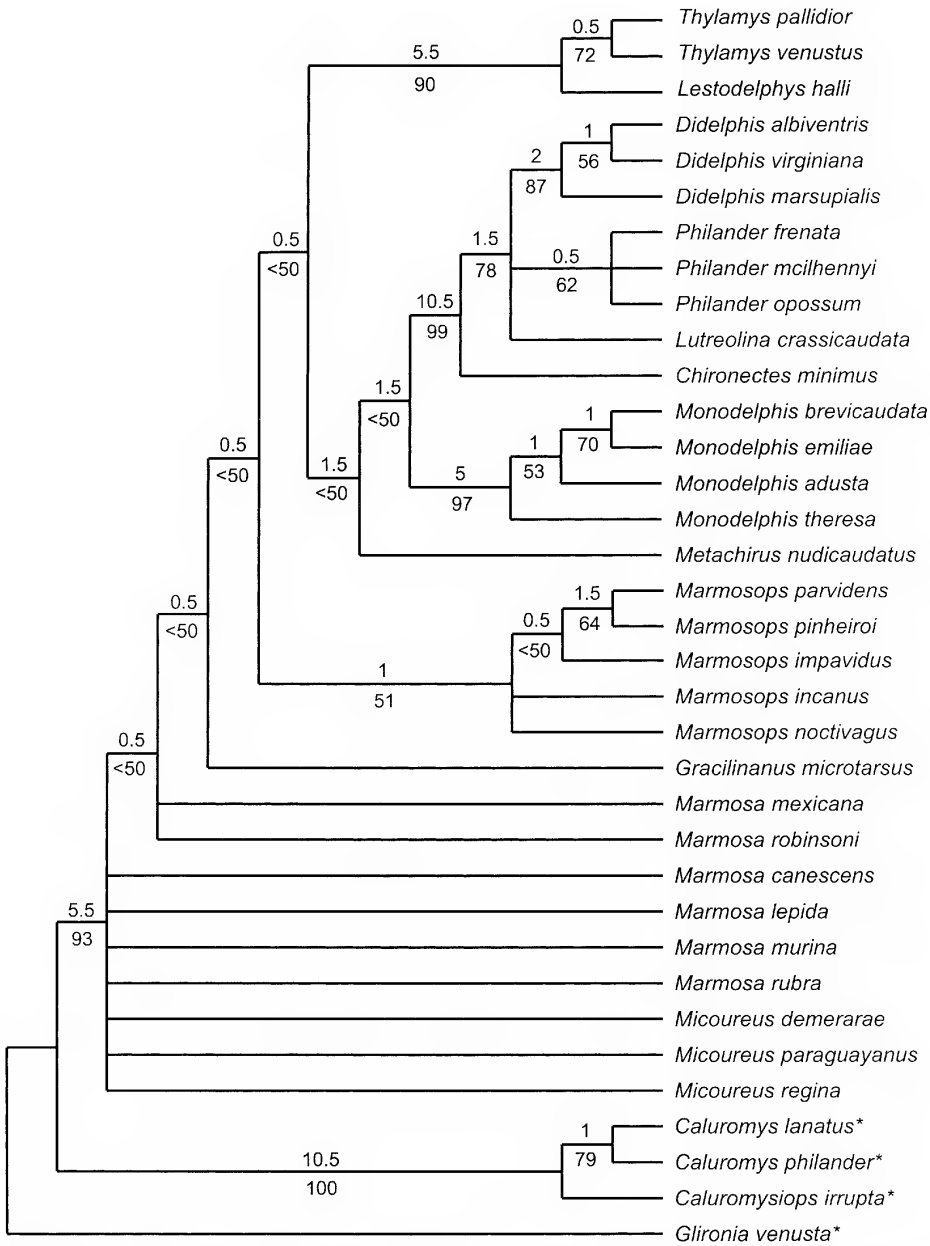


Fig. 17. Strict consensus of 2161 equally most-parsimonious trees obtained by a heuristic analysis of nonmolecular characters described in this report (see table 4 for summary dataset characteristics and tree statistics). Bremer support and bootstrap values are provided above and below each branch, respectively. Outgroup taxa are indicated with asterisks.

ter-species pair *M. parvidens* + *M. pinheiroi*. Moving up the tree, *Lestodelphys* clusters with a monophyletic pair of *Thylamys* species, and that group (*Lestodelphys* + *Thylamys*) is sister to a clade that consists successively of *Metachirus*, *Monodelphis*, and the large $2n = 22$ opossums. Relationships among the four included species of *Monodelphis* are resolved in the sequence (*M. theresa* (*M. adusta* (*M. brevicaudata* + *M.*

emiliae))). Among the large $2n = 22$ opossums, *Chironectes* is basal to an unresolved polytomy of *Lutreolina* + *Philander* + *Didelphis*, and the latter two genera are resolved as reciprocally monophyletic groups. Relationships among the three species of *Philander* are unresolved due to lack of data (*P. mcilhennyi* and *P. opossum* are not distinguishable by the nonmolecular characters scored for this analysis), but relationships among *Didelphis* species are resolved in the sequence (*D. marsupialis* (*D. albiventris* + *D. virginiana*)).

Decay (Bremer) analyses reveal that most ingroup nodes are not strongly supported by nonmolecular characters. Eleven didelphine clades (55% of the total depicted in fig. 17) collapse in trees that are only one step longer, and an additional five clades (25%) collapse in trees that are two steps longer. Only four ingroup nodes (20%) have larger decay values: the didelphine root node, *Monodelphis*, the large $2n = 22$ opossum group, and *Lestodelphys* + *Thylamys*. Bootstrap resampling suggests a similar pattern of support, with the latter four nodes having the highest representation (90–99%) among most-parsimonious trees computed from 1000 pseudoreplicated datasets.

MOLECULAR DATA AND ANALYTIC RESULTS

We sequenced a segment of IRBP exon 1 that is 1158 base pairs long and begins 139 base pairs downstream from the start codon of the homologous human RBP3 gene (GenBank accession NM 002900). We were unable to obtain sequence from the first 20 base pairs of this fragment in one specimen of *Gracilinanus microtarsus* (MVZ 182055), from the first three base pairs in another specimen of the same species (MVZ 182056), and from the first 24 base pairs of *Thylamys pallidior* (FMNH 162495). In addition, the final 426 base pairs were not sequenced from one of our two specimens of *Philander mcilhennyi* (AMNH 272818). With these exceptions, all IRBP sequences obtained in this study were of the same length, and no internal gaps were needed to align them with one another or with the didelphid sequences previously reported by Jansa and Voss (2000). All didelphid IRBP sequences translate to open reading frame. We found no compelling evidence for sequence saturation in our previous IRBP dataset (Jansa and Voss, 2000: fig 8), nor is there any indication of saturation for either transitions or transversions at any codon position in our current data.

Uncorrected pairwise divergence among nonconspecific didelphid sequences analyzed in this study ranged from 0.7 to 5.8% (slightly exceeding the range of values previously reported by Jansa and Voss, 2000). Among the conspecific material newly sampled here (appendix 2), our duplicate specimens of *Caluromys philander*, *Marmosa canescens*, *Micoureus paraguayanus*, *Monodelphis brevicaudata*, and *Thylamys venustus* had identical sequences. Two specimens of *Marmosops incanus* from the same locality in southeastern Brazil differed by a single base substitution, as did two specimens of *Micoureus regina* from opposite banks of the Rio Juruá in western Brazil. Two specimens of *Marmosa robinsoni* from Panama differed at four base positions, whereas two specimens of *Marmosa mexicana* from Guatemala differed by a single substitution. Two new sequences of *Marmosa murina* from Surinam differed from each other at two base positions, but these specimens differed from previously sequenced Peruvian material (analyzed by Jansa and Voss, 2000) by four to six substitutions.

After condensing redundant didelphid sequences to single OTUs, we obtained a primary data matrix (IRBP1) of 49 unique terminals coded for 1158 base pairs. Of the 56,742 cells in this matrix, only 473 (0.8%) are coded as missing due to lack of sequence (see above). Further data condensation for the purpose of treating species as OTUs resulted in a second matrix (IRBP2) of 35 terminals coded for 1158 base pairs. The sequence for *Philander mcilhennyi* in IRBP2 includes 426 base pairs from MUSM 13299 that were coded as missing from AMNH 272818, and the sequence for *Gracilinanus microtarsus* includes 17 base pairs from MVZ 182056 that were coded as missing from MVZ 182055. Therefore, IRBP2 has only 27 cells (<0.1%) coded as missing. The number of matrix cells scored with IUPAC

TABLE 4
Dataset Characteristics and Tree Statistics from Parsimony Analyses of Three Didelphid Datasets

	Nonmolecular	IRBP1	IRBP2	Combined
Number of terminal taxa[a]	35	49	35	35
Number of informative characters	66	165	149	215
Number of MPTs[b]	2161	252	27	34
Tree length[c]	158	431	398	567
Consistency index (CI)[d]	0.55	0.64	0.64	0.59
Retention index (RI)	0.85	0.88	0.84	0.83
Resolved ingroup nodes[e]	20	25	25	23
Total ingroup support[f]	42	97	105	138

[a]Terminal taxa (OTUs) are species in the nonmolecular, IRBP2, and combined datasets, but they consist of unique sequences (some of which are conspecific) in the IRBP1 dataset (see Materials and Methods).

[b]Equally most-parsimonious trees recovered by heuristic searches as described in Materials and Methods.

[c]Including autapomorphies.

[d]Excluding autapomorphies.

[e]Excluding nodes that resolve relationships among conspecific sequences in the IRBP1 analysis.

[f]Sum of Bremer support values over ingroup nodes illustrated in figures 17, 18, and 21 (i.e., excluding nodes that resolve relationships among conspecific sequences in the IRBP1 analysis).

ambiguity codes is 59 (0.1%) in IRBP1, but 103 cells (0.2%) are ambiguity-coded in IRBP2 due to intraspecific polymorphisms resulting from taxon condensation.

The base-compositional profile for these didelphid sequences is similar to that for the marsupial and placental sequences previously reported by Jansa and Voss (2000): base composition across all codon positions is approximately even among didelphids, but exhibits a slight bias toward guanine and cytosine (54.9–58.7%). First and third positions show the highest GC content (63.4–66.8% at first positions, 61.5–65.5% at third positions), whereas second positions show equivalent bias towards adenine and thymine (the range of AT content at second positions is 60.9–61.1%). Because taxon differences in base composition can compromise phylogenetic inference, we assessed IRBP1 and IRBP2 for stationarity using Chi-square tests. By this criterion, no codon position in either matrix violates base-compostitional stationarity (IRBP1: first positions: $\chi^2 = 5.87$, $p = 1.0$; second positions: $\chi^2 = 6.59$, $p = 1.0$; third positions: $\chi^2 = 18.98$, $p = 1.0$; df = 144 for each test; IRBP2: first positions: $\chi^2 = 3.62$, $p = 1.0$; second positions: $\chi^2 = 3.38$, $p = 1.0$; third positions: $\chi^2 = 14.05$, $p = 1.0$; df = 102 for each test).

Parsimony Analysis of IRBP Sequence Data

A heuristic analysis of IRBP1 (with 165 informative characters) recovered 252 equally most-parsimonious trees, most of which differ only with respect to alternative branching patterns among conspecific terminals. By contrast, a heuristic analysis of IRBP2 (with 149 informative characters) recovered only 27 equally most-parsimonious trees. Although the two sets of minimal-length trees supported by these datasets differ slightly in length and other statistics (table 4), their strict consensus topologies (rooted with *Glironia*) depict identical patterns of interspecific relationships (fig. 18). By comparison with our nonmolecular results, the same branching topology among outgroup taxa was obtained (with *Caluromysiops* sister to *Caluromys lanatus* + *C. philander*), but the IRBP data support a pattern of ingroup relationships that differs in many respects from that supported by morphology.

At the base of the didelphine radiation is an unresolved polytomy consisting of four groups: (1) *Marmosa canescens*; (2) other species of *Marmosa* plus *Micoureus*; (3) *Monodelphis*; and (4) other didelphines. This situation results from character conflict rather than lack of data because equally most-par-

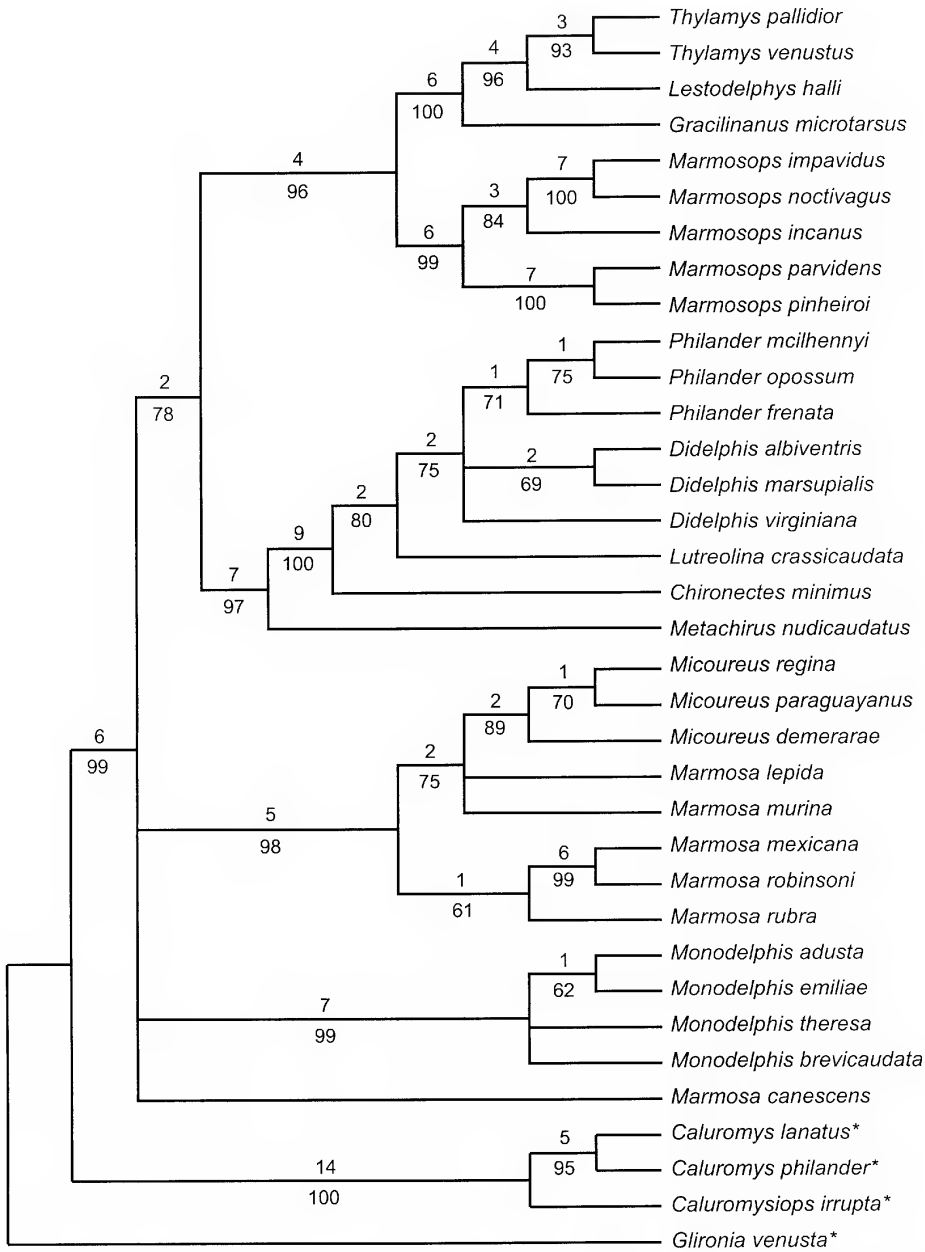


Fig. 18. Strict consensus of 252 equally most-parsimonious trees obtained by a heuristic analysis of IRBP sequences described in this report (see table 4 for summary dataset characteristics and tree statistics). Bremer support and bootstrap values are provided above and below each branch, repectively. For simplicity, conspecific sequences (analyzed separately in PAUP*) have been condensed to single terminals in this diagram. Outgroup taxa are indicated with asterisks. All parsimony-equivalent resolutions of the basal ingroup polytomy are shown in figure 19A–E.

simonious trees with nonzero branch lengths resolve the relationships among these clades differently (fig. 19). Although it is noteworthy that a sister-group relationship of *Marmosa canescens* with the "other *Marmosa*" + *Micoureus* clade is among such parsimony-equivalent resolutions, the monophyly of *Marmosa* (as that genus is currently recog-

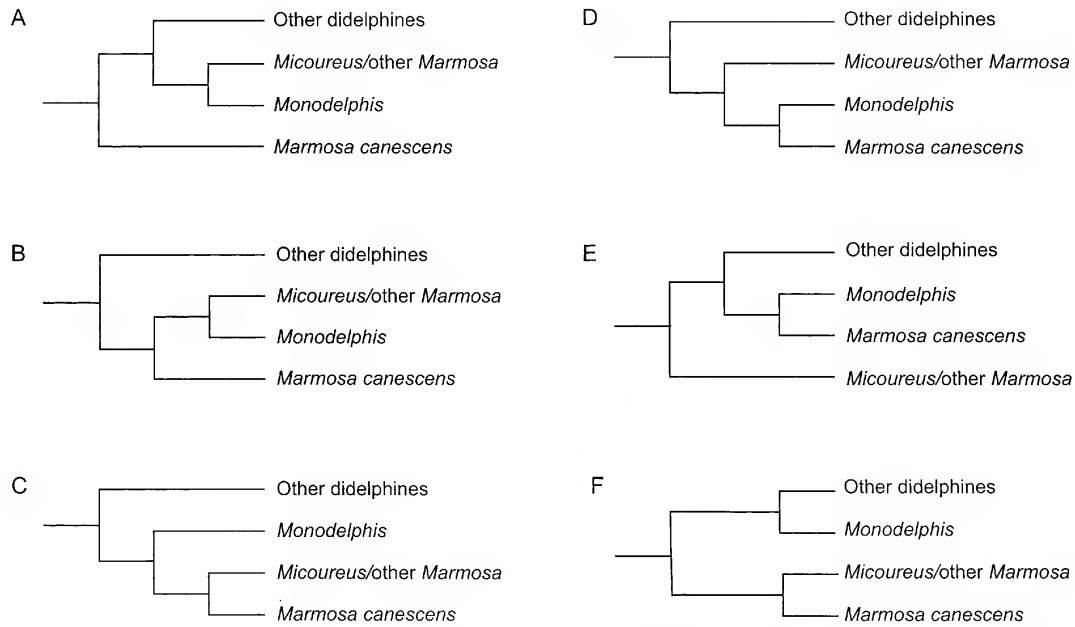


Fig. 19. All equally most-parsimonious resolutions of the basal didelphine polytomy in figures 18 and 21. **A,** Resolution supported by 72 most-parsimonious trees (MPTs) from the IRBP1 analysis and 6 MPTs from the IRBP2 analysis; **B,** resolution supported by 72 MPTs from the IRBP1 analysis and 6 MPTs from the IRBP2 analysis; **C,** resolution supported by 36 MPTs from the IRBP1 analysis and 3 MPTs from the IRBP2 analysis; **D,** resolution supported by 36 MPTs from the IRBP1 analysis, 6 MPTs from the IRBP2 analysis, and 8 MPTs from the combined analysis; **E,** resolution supported by 36 MPTs from the IRBP1 analysis, 6 MPTs from the IRBP2 analysis, and 8 MPTs from the combined analysis; **F,** resolution supported by 18 MPTs from the combined analysis only.

nized) is not consistent with any topology supported by IRBP. Equally noteworthy is that *Monodelphis* is most-parsimoniously resolved as the sister group of *Marmosa canescens* (fig. 19D, E), of "other *Marmosa*" + *Micoureus* (fig. 19A, B), or of a group consisting of both clades (fig. 19C); it is never resolved as the sister taxon of the remaining didelphines in this analysis.

Within the "other *Marmosa*" + *Micoureus* group, species of *Micoureus* form a clade but species of *Marmosa* do not. Instead, *Marmosa murina* and *M. lepida* cluster with *Micoureus*, whereas *Marmosa rubra*, *M. mexicana*, and *M. robinsoni* form another subgroup. Most relationships among these taxa are resolved in the consensus topology, with the exception of a polytomy involving *Micoureus*, *Marmosa murina*, and *M. lepida* that results from lack of data. Species relationships within *Monodelphis* are also incompletely resolved, and they are partially in conflict with our nonmolecular results (wherein *M. brevicaudata* and *M. emiliae* were recovered as sister species). In this analysis, *M. emiliae* clusters with *M. adusta*, whereas the relationships of *M. brevicaudata* and *M. theresa* are unresolved due to lack of data.

The group that contains the remaining didelphines (equivalent to clade H of Jansa and Voss, 2000) consists of two large subgroups. The first of these (clade C; op. cit.) contains four small-bodied "marmosine" genera in the sequence (*Marmosops* (*Gracilinanus* (*Lestodelphys* + *Thylamys*))), whereas the second (clade G; op. cit.) contains five large-bodied genera in the sequence (*Metachirus* (*Chironectes* (*Lutreolina* (*Philander* + *Didelphis*)))). Within clade C, both of the genera represented by multiple species—*Marmosops* and *Thylamys*—are resolved as monophyletic groups. By contrast with the relationships among species of *Marmosops*

recovered from our nonmolecular data, however, a clade containing two miniature species (*M. parvidens* + *M. pinheiroi*) is basal to a group of larger species in the sequence (*M. incanus* (*M. impavidus* (*M. noctivagus*))). *Philander* and *Didelphis* are each represented by three species in clade G, but only the monophyly of the former genus is supported. Whereas a monophyletic *Didelphis* is supported by our nonmolecular data, equally parsimonious IRBP trees support *D. virginiana* as the sister group of *D. albiventris* + *D. marsupialis* on the one hand or of *Philander* on the other.

Decay analyses of the IRBP data indicate that only 5 (20%) of the 25 ingroup nodes resolved in this strict consensus topology collapse in trees that are one step longer; another 6 nodes (24%) collapse in trees that are two steps longer, and 2 more nodes (8%) collapse in trees that are three steps longer. The remaining 12 nodes (48%) have decay values >3 and are also supported by very high bootstrap values (>95%).

Likelihood Analysis of IRBP Sequences

The best-fit model of sequence evolution for IRBP2 is one with equal base frequencies and different rates of transitions and transversions. There is no significant difference in log-likelihood scores for these data between a model that assumes equal base frequencies (JC69) and one that allows base frequencies to differ (F81; $-2 \ln \Lambda = 2.7803$, df = 3, $p = 0.43$). However, there is a significant improvement in log-likelihood scores between the simple JC69 model and one that allows for two different substitution types (K2P; $-2 \ln \Lambda = 204.26$, df = 1, $p << 0.01$). A model that allows for three substitution types (K3P) offered no significant improvement in log-likelihood score over the K2P model ($-2 \ln \Lambda = 0.2090$, df = 1, $p = 0.65$).

We next evaluated whether the fit of K2P could be improved by adding parameters for site-specific rate heterogeneity. A model that assumes different rates among sites following a Γ distribution (K2P + Γ Yang, 1994) fits the data better than does the single-rate alternative ($-2 \ln \Lambda = 229.02$; df = 1; $p << 0.01$), and allowing for a proportion of invariable sites further improves the goodness of fit (K2P + Γ + I; $-2 \ln \Lambda = 8.41$, df = 1, $p < 0.01$); the shape parameter for the Γdistribution was estimated as 0.84, and the proportion of invariant sites was estimated as 0.51. Based on a nonsignificant test result assessing the fit of the above model with and without a molecular clock ($-2 \ln \Lambda = 36.31$; df = 33; $p = 0.32$), the simpler version (with a molecular clock) cannot be rejected for these sequence data.

A heuristic search discovered 18 topologies that were equally likely ($-\ln L = 4180.49$) under the chosen model of sequence evolution (K2P + Γ + I with a molecular clock). Although the inferred position of the root in these maximum-likelihood estimates was on the branch leading to clade G, the same topologies rooted to be consistent with our assumption of ingroup monophyly do not have significantly different log-likelihood scores (as determined by the nonparametric test suggested by Shimodaira and Hasegawa, 1999), so the strict consensus of the latter trees is depicted here (fig. 20). This topology is nearly identical to, and completely congruent with, the most-parsimonious strict consensus. The only difference concerns the placement of *Marmosa canescens*, which is resolved (with 47% bootstrap support) as the sister taxon to clade J under maximum likelihood, rather than as part of the four-fold polytomy in the maximum-parsimony tree (fig. 18). Maximum-likelihood bootstrap values are strongly correlated with homologous parsimony bootstrap values as determined by a Spearman rank correlation test ($r_S = 0.84$, $p << 0.01$, df = 27).

ANALYSIS OF THE COMBINED DATA

Heuristic parsimony analysis of the combined-data matrix (nonmolecular characters + IRBP2) discovered 34 minimal-length trees, which we rooted with *Glironia* to compute their strict consensus. The resulting topology (fig. 21) closely resembles our IRBP results (fig. 18) but is less resolved due to character conflict within certain genera. The same four didelphine groups form a basal polytomy in both the IRBP and combined-data trees, but a different set of parsimony-equivalent alternative resolutions are supported by the combined analysis (fig. 19). Among them

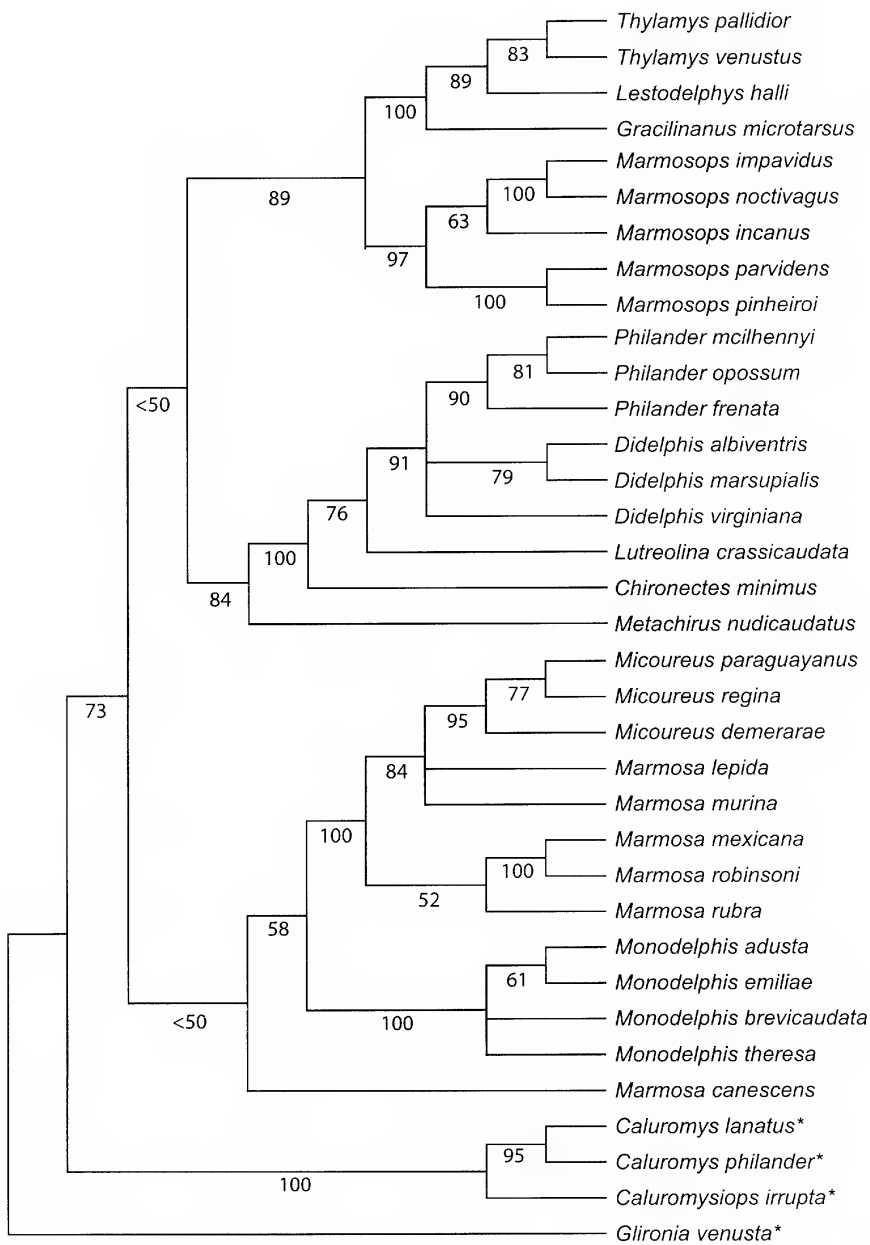


Fig. 20. Strict consensus of 18 maximum-likelihood trees under the best-fit model of IRBP sequence evolution, rooted to be consistent with our assumption of ingroup (didelphine) monophyly (see text). Bootstrap support values are shown below each branch. Outgroup taxa are indicated with asterisks.

is one in which *Monodelphis* is sister to clade H ("other didelphines"; fig. 19F).

Clades C, G, and H are all recovered in the combined analysis. However, whereas clade C has the same internal branching structure as it did in the taxon-dense IRBP parsimony tree, the internal structure of clade G in the combined analysis differs because *Didelphis* and *Philander* are resolved as reciprocally monophyletic groups. The principal loss of resolution in the combined-data consensus topology occurs within two clades (the "other *Marmosa*" + *Micoureus* cluster and *Monodelphis*) where nonmolecular and

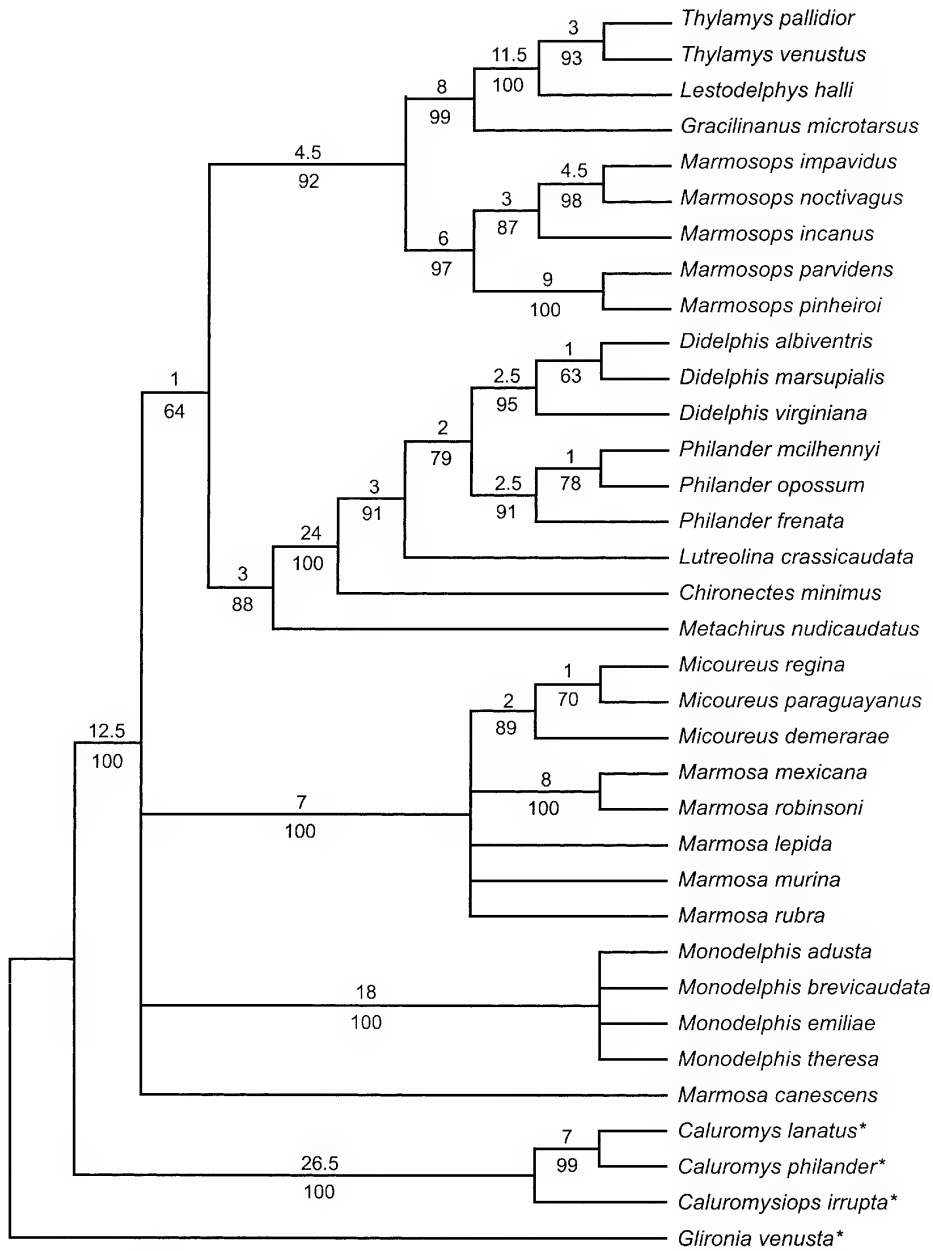


Fig. 21. Strict consensus of 34 equally most-parsimonious trees obtained by a heuristic analysis of the combined data (nonmolecular characters plus IRBP2) described in this report. Bremer support and bootstrap values are provided above and below each branch, respectively. Outgroup taxa are indicated with asterisks. Parsimony-equivalent resolutions of the basal ingroup polytomy are illustrated in figure 19D, E, and F. Parsimony-equivalent resolutions of the "other *Marmosa*" + *Micoureus* polytomy are shown in figure 22.

sequence data provide conflicting estimates of relationships.

Alternative parsimony-equivalent resolutions of the five-fold polytomy within the "other *Marmosa*" + *Micoureus* clade do not include any topology in which the two genera are resolved as reciprocally monophyletic groups (fig. 22). Either *Marmosa murina* and *M. lepida* cluster with *Micoureus* (fig. 22A–C) or those three taxa are joined with *M. rubra* (fig. 22D) or a group composed of *M. mexicana* + *M. robinsoni* + *M. rubra* clusters with *Micoureus* (fig. 22E). All possible topologies in which "other *Marmosa*" species and *Micoureus* are reciprocally monophyletic are two steps longer than these alternatives.

Most of the 23 resolved ingroup nodes in the combined-data consensus topology are at least moderately well supported. Only three nodes (13%) collapse in trees that are one step longer, two additional nodes (9%) collapse in trees that are two steps longer, and seven more nodes (30%) collapse in trees that are three steps longer. The remaining 11 nodes (48% of the total) have Bremer support values >3 and also have uniformly high bootstrap support (92–100%).

DISCUSSION

Dataset Comparisons

The three datasets analyzed separately in this study differ in several quantitative characteristics that are often interpreted as indicators of phylogenetic utility, including number of equally most-parsimonious trees, ensemble consistency index, ensemble retention index, number of resolved nodes in the strict consensus, and total support (table 4). However, dataset differences in homoplasy estimates (CI, RI) are small, and differences in numbers of equally most-parsimonious trees, numbers of resolved nodes, and total support are plausibly explained by informative-characters-to-taxon ratios (approximately 1.9 in the nonmolecular dataset versus 3.4–4.3 in the IRBP datasets). In effect, IRBP simply provides more data per branch for resolving didelphid relationships than do nonmolecular characters.

Although the nonmolecular and IRBP consensus trees (figs. 17, 18) exhibit obvious to-

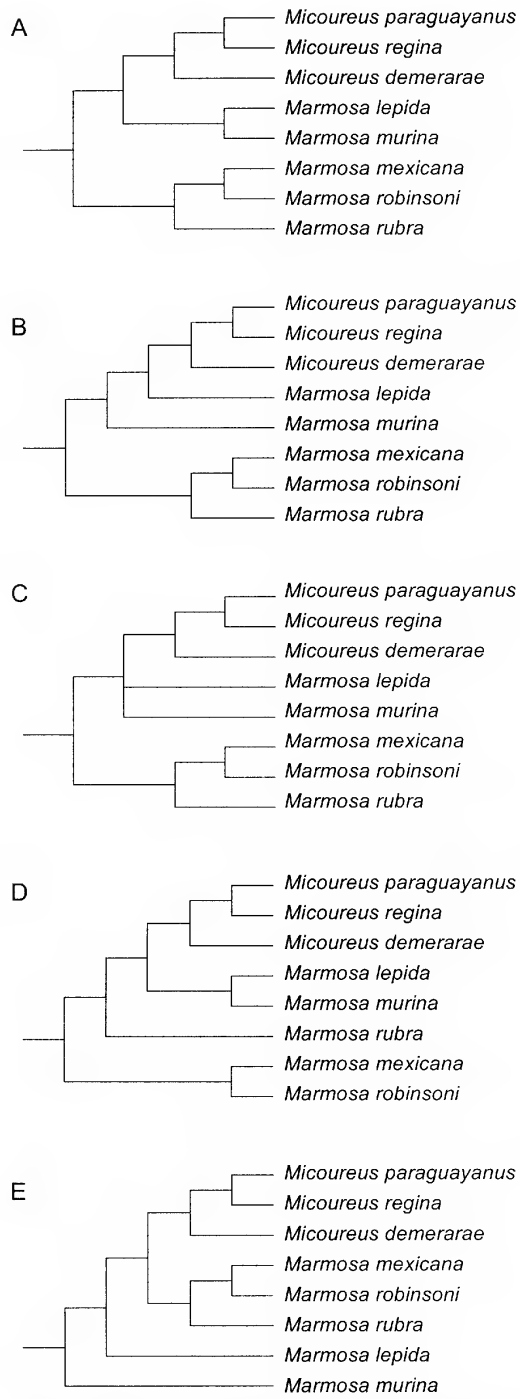


Fig. 22. Alternative resolutions of the "other *Marmosa*" + *Micoureus* clade based on parsimony analysis of the combined (nonmolecular + IRBP2) data. Among the 34 equally most-parsimonious trees whose strict consensus is illustrated in figure 21, resolution A is represented by 10 trees, B by 4 trees, C by 10 trees, D by 6 trees, and E by 4 trees.

pological differences that imply substantial phylogenetic conflict, node-by-node comparisons of Bremer support and bootstrap values suggest otherwise. No clade that is even moderately well supported (with Bremer support >2 and/or bootstrap values >70%) in either analysis is incongruent with any equivalently supported node in the other. Instead, every example of conflicting relationships revealed by these separate analyses involves weak support from one or both datasets. Such results are consistent with our previous assessment (Jansa and Voss, 2000) that examples of "hard" incongruence—incompatibility between well-defined patterns of morphological versus molecular synapomorphy—are rare among didelphids. In fact, examples of hard incongruence (as opposed to diffuse homoplasy) seem to be nonexistent in the present study.

Nonmolecular Evidence for Didelphine Relationships

None of the ingroup relationships that are strongly supported (with Bremer support >3 and bootstrap values >90%) by our analysis of nonmolecular characters is controversial. Monophyly of the subfamily Didelphinae, monophyly of the large $2n = 22$ opossum group, and monophyly of *Lestodelphys* + *Thylamys* were all previously suggested by Creighton (1984) and Reig et al. (1987) based on their independent analyses of nonmolecular data, despite the fact that those studies differed significantly from each other and from ours in character composition. Apparently, these clades are robust to alternative criteria for nonmolecular character choice. Monophyly of the genus *Monodelphis* has been assumed (at least implicitly) by morphological systematists, but it has not previously been tested by phylogenetic analyses of nonmolecular data. All four groups (Didelphinae, the large $2n = 22$ opossums, *Lestodelphys* + *Thylamys*, and *Monodelphis*) are also strongly supported by parsimony analyses of IRBP sequences (Jansa and Voss, 2000), and they are consistent with phylogenetic interpretations of DNA-DNA hybridization experiments (Kirsch et al., 1997). In effect, these relationships seem to be established beyond any serious doubt, despite some conflicting results from cytochrome *b* (Patton et al., 1996).[11]

The only other didelphine clade that is even moderately well supported by nonmolecular character data is the genus *Didelphis*. By virtue of long acceptance this taxon has implicitly been assumed to be monophyletic, but no prior morphological study has tested generic monophyly. Instead, monophyly of *Didelphis* has previously been supported by analyses of cytochrome-*b* sequences (Patton et al., 1996) and by DNA-DNA hybridization results (Kirsch et al., 1997). Although IRBP sequences do not resolve *Didelphis* as a clade, neither do they (or any other published data) provide support for any incongruent pattern of relationships (Jansa and Voss, 2000). Therefore, monophyly of *Didelphis* is another noncontroversial result.

Among those didelphine relationships that are weakly supported by nonmolecular characters, several are consistent with the results of previous or current phylogenetic results based on other data including (1) the monophyly of *Thylamys* (see Kirsch et al., 1997), (2) a sister-group relationship between *Didelphis* and *Philander* (see Patton et al., 1996; Kirsch et al., 1997; Palma and Spotorno, 1999; Jansa and Voss, 2000), (3) the monophyly of *Didelphis* + *Philander* + *Lutreolina* (see Creighton, 1984; Kirsch et al., 1997; Palma and Spotorno, 1999; Jansa and Voss, 2000), (4) the monophyly of *Marmosops* (see Jansa and Voss, 2000), and (5) a sister-group relationship between *Marmosops parvidens* and *M. pinheiroi*. Although results that are incongruent with some of these relationships have also been reported, none is compelling. For example, Reig et al. (1987) depicted *Chironectes* as the nearest extant sister group of *Didelphis* in their summary cladogram (op. cit.: fig. 68), but *Philander* and/or *Lutreolina* were actually found to be more closely related to *Didelphis* in most of their parsimony analyses. Likewise, DNA-DNA hybridization results showing *Gracilinanus* nested inside the genus *Mar-*

[11] Parsimony and neighbor-joining analyses reported by Patton et al. (1996) do not support the monophyly of Didelphinae, but cytochrome *b* evolves much more quickly than IRBP and appears to be substitution-saturated at this level of taxonomic comparison (Jansa and Voss, 2000: fig. 12).

mosops (see Kirsch and Palma, 1995; Kirsch et al., 1997) are now unambiguously attributable to taxonomic misidentifications.[12]

Therefore, 10 out of the 20 resolved ingroup nodes in our nonmolecular strict consensus tree are both supported by independent analyses of other datasets and lack compelling contradictory evidence. The remaining 10 nodes, all weakly supported, are problematic because they are contradicted by other datasets, including the IRBP and combined analyses discussed below. Because only ad hoc explanations are possible for phylogenetic conflicts involving trivial character support, we do not discuss such problems here.

Effects of Denser Taxon Sampling

Denser taxon sampling is often suggested as one way to improve the accuracy of phylogenetic analyses (Wheeler, 1992; Graybeal, 1998; Hillis, 1998; Zwickl and Hillis, 2002; Pollock et al., 2002), but the result in any particular case is not predictable because adding taxa can increase homoplasy and reduce—rather than improve—phylogenetic resolution (Novacek, 1991). Even in the absence of homoplasy, however, adding taxa scored for the same set of characters tends to decrease average nodal support because synapomorphies are subdivided among a larger number of internal branches (Horovitz, 1999). Therefore, neither better resolution nor higher confidence in the topology of recovered trees is a necessary consequence of sampling more taxa.

[12] According to J.A.W. Kirsch (in litt., 27 October 2002), the samples of "*Gracilinanus agilis*" from which DNA was extracted for hybridization experiments were NK 23117 and NK 23191 from the tissue collection of the Museum of Southwestern Biology (University of New Mexico, Albuquerque). We borrowed the corresponding morphological voucher specimens (MSB 67020 and MSB 87094, respectively) and determined that they are examples of *Marmosa ocellata* Tate (1931), a nominal taxon that is currently regarded as a junior synonym of *Marmosops dorothea* (Thomas, 1911). These misidentifications explain the paradox remarked by Kirsch and Palma (1995: 414) that "*M. dorothea* proved nearly indistinguishable from *Gracilinanus agilis*" by thermal elution of scnDNA heteroduplexes. According to Kirsch and Palma (1995), their specimens were identified using keys in Hershkovitz (1992b), but the only key provided in that paper does not accurately diagnose *Gracilinanus* from *Marmosops*.

Thus, some relationships that were completely resolved in our previous analysis of didelphid IRBP sequences (Jansa and Voss, 2000) are not resolved in the present taxon-dense analysis based on the same set of characters. In particular, clade J (fig. 1) was recovered when we sampled only two species each of *Marmosa* and *Monodelphis* and one species of *Micoureus*, but that pattern of relationships is only one of several parsimony-equivalent resolutions of a four-fold polytomy that results when those genera are more densely sampled (figs. 18, 19). Among ingroup nodes common to both analyses, nodal support statistics are generally lower in our current results based on sequences from 31 didelphine species than in our previous study of only 18 didelphine species (table 5).

Whereas denser taxon sampling might be considered counterproductive in these respects, new information has been obtained about the relationships of species that were not included in our previous study. Adding those taxa effectively tested the monophyly of six ingroup genera (*Marmosa*, *Marmosops*, *Micoureus*, *Monodelphis*, *Philander*, *Thylamys*) as well as the deeper branching structure of didelphine phylogeny. The fact that *Marmosa* is not demonstrably monophyletic, and the discovery that *M. canescens* has a destabilizing effect on basal didelphine relationships, are both important results that underscore the need for denser sampling of other genera that remain sparsely represented in our datasets (see below).

Likelihood Analysis

Phylogenetic analyses based on explicit models of sequence evolution, typically implemented in the context of maximum-likelihood estimation, are often recommended as solutions for problems caused by transition/transversion bias, uneven base composition, grossly unequal branch lengths, and other phenomena that have been shown to cause inaccurate parsimony reconstructions of simulated phylogenies (Felsenstein, 1978; Huelsenbeck and Hillis, 1993; Huelsenbeck, 1995). Whether or not such problems are effectively ameliorated by maximum-likelihood analyses of real datasets—for which crucial model parameters needed to calculate

TABLE 5
Bremer Support for Nodes Common to Parsimony Analyses of Two IRBP Datasets

	Jansa & Voss (2000)[a]	Present study[b]	Difference[c]
Thylamys + *Lestodelphys* (= clade A)	2.0	4.0	+2.0
Clade A + *Gracilinanus* (= clade B)	7.0	6.0	−1.0
Marmosops noctivagus + *M. impavidus*	11.0	7.0	−4.0
Marmosops	8.0	6.0	−2.0
Clade B + *Marmosops* (= clade C)	5.0	4.0	−1.0
Didelphis albiventris + *D. marsupialis*	2.0	2.0	0.0
Didelphis + *Philander* (= clade D)	2.0	2.0	0.0
Clade D + *Lutreolina* (= clade E)	2.0	2.0	0.0
Clade E + *Chironectes* (= clade F)	9.0	9.0	0.0
Clade F + *Metachirus* (= clade G)	8.0	7.0	−1.0
Clade C + Clade G (= clade H)	2.0	2.0	0.0
Marmosa + *Micoureus* (= clade I)	9.0	5.0	−4.0
Didelphinae (ingroup root)	7.0	6.0	−1.0
Totals	74.0	62.0	−12.0

[a]Topology reproduced in figure 1.
[b]Results from analysis of IRBP1 (fig. 18).
[c]Net result of denser taxon sampling in the present study.

log-likelihood scores are unknown—is the subject of current controversy (Steel and Penny, 2000). Nevertheless, maximum likelihood provides an alternative optimality criterion for phylogenetic inference that now enjoys wide currency and merits comparison with parsimony-based results when a common model can plausibly be fitted to character data.

Because didelphid IRBP sequences are not conspicuously problematic in any of the ways that are commonly thought to bias maximum-parsimony procedures, it is not surprising that maximum likelihood yields a consensus topology that is almost identical to (and fully congruent with) the consensus of most-parsimonious trees. By implication, phylogenetic inference from these data is robust to at least this alternative choice of optimality criteria.

Effects of Combining Nonmolecular and IRBP Data

Given the absence of strong nodal conflict between the nonmolecular and IRBP consensus topologies, together with the large dataset difference in numbers of informative characters, it was to be expected that our combined-data consensus (fig. 21) would closely resemble the IRBP topology (fig. 18). In fact, the small net loss of resolution resulting from data combination (two ingroup nodes) suggests a substantial degree of character agreement and/or complementarity in the combined data, as does the result that total nodal support in the combined analysis is almost equal to the sum of total support from the separate analyses (table 4). Node-by-node comparisons of support statistics between the IRBP and combined-data trees, however, provide a better picture of the effects of data combination on nodes common to both topologies (table 6).

Out of 22 ingroup nodes present in both trees, 7 show no change in Bremer support, 4 are less strongly supported in the combined analysis than they were in the IRBP tree, and 11 are more strongly supported by the combined data than by IRBP alone. As expected, nodes showing the largest increases in Bremer support are those most strongly supported in each separate analysis (*Thylamys* + *Lestodelphys*, clade F, *Monodelphis*, Didelphinae). However, some nodes that were not present in the nonmolecular consensus topology (fig. 17) also exhibit higher support in the combined analysis than in the IRBP tree, including clade B, clade C, *Marmosa mexicana* + *M. robinsoni*, and "other *Marmosa*" + *Micoureus*. In addition, Bremer

TABLE 6
Bremer Support for Nodes Common to Parsimony Analyses of IRBP2 and Combined Datasets

	IRBP2[a]	Combined[b]	Difference[c]
Thylamys	3.0	3.0	0.0
Thylamys + *Lestodelphys* (= clade A)	4.0	11.5	+7.5
Clade A + *Gracilinanus* (= clade B)	7.0	8.0	+1.0
Marmosops impavidus + *M. noctivagus*	6.0	4.5	−1.5
Marmosops impavidus + *M. noctivagus* + *M. incanus*	3.0	3.0	0.0
Marmosops parvidens + *M. pinheiroi*	7.0	9.0	+2.0
Marmosops	6.0	6.0	0.0
Clade B + *Marmosops* (= clade C)	4.0	4.5	+0.5
Didelphis albiventris + *D. marsupialis*	2.0	1.0	−1.0
Philander mcilhennyi + *P. opossum*	1.0	1.0	0.0
Philander	2.0	2.5	+0.5
Didelphis + *Philander* (= clade D)	2.0	2.0	0.0
Lutreolina + clade D (= clade E)	2.0	3.0	+1.0
Chironectes + clade E (= clade F)	14.0	24.0	+10.0
Metachirus + clade F (= clade G)	7.0	3.0	−4.0
Clade C + clade G (= clade H)	2.0	1.0	−1.0
Micoureus regina + *M. paraguayanus*	1.0	1.0	0.0
Micoureus	2.0	2.0	0.0
Marmosa mexicana + *M. robinsoni*	7.0	8.0	+1.0
"Other *Marmosa*" + *Micoureus*	6.0	7.0	+1.0
Monodelphis	7.0	18.0	+11.0
Didelphinae (ingroup root)	6.0	12.5	+6.5
Totals	101.0	135.5	+34.5

[a] Some Bremer support values differ from those illustrated in figure 18, which shows the results of analyzing IRBP1.
[b] See figure 21.
[c] Net result of combining IRBP2 and nonmolecular datasets.

support for some nodes in the combined-data analysis that are common to both the nonmolecular and IRBP topologies exceeds the sum of support values from the separate analyses. For example, Bremer support for *Monodelphis* in the combined analysis is six steps more than the sum of Bremer support for this clade in the nonmolecular and IRBP analyses. The discovery of such hidden branch support is a not-infrequent result of combining datasets and a compelling reason to explore the consequences of simultaneous analysis whether or not different data partitions are significantly incongruent (Gatesy et al., 1999b).

The *Marmosa* Problem

Conspicuously absent from these results is any support for the monophyly of *Marmosa* in any of the past or current usages of that name (table 7). At worst (sensu Tate, 1933) the genus is polyphyletic, but even at best (sensu Gardner and Creighton, 1989) it appears to be no more than a paraphyletic collection of plesiomorphic small didelphines. In order to preserve a monophyletic generic classification, some taxonomic changes are clearly required.

The phylogenetic classification of "*Marmosa*" *canescens* was previously discussed by Engstrom and Gardner (1988) in the context of their unexpected discovery of a derived $2n = 22$ karyotype in a genus otherwise characterized by the plesiomorphic $2n = 14$ complement (see table 2). On the basis of morphological comparisons, they rejected a close relationship of *canescens* with either the large $2n = 22$ opossums or with *Monodelphis* ($2n = 18$), concluding that centric fissioning occurred independently in *canescens*. We agree that there is no compelling morphological evidence for a close relationship of *canescens* with other didelphids that have high diploid numbers. However, there

TABLE 7
Results of Parsimony Analyses with Topological Constraints[a]

	Parsimony cost[b]			
	Nonmolecular	IRBP1	IRBP2	Combined
Marmosa sensu Tate (1933)[c]	10.5	20.0	21.0	29.0
Marmosa sensu Reig et al. (1985)[d]	5.5	18.0	18.0	22.5
Marmosa sensu Gardner and Creighton (1989)[e]	2.5	8.0	9.0	11.0

[a]Constraints were imposed as hypotheses of monophyly for each listed taxon.

[b]Cost was calculated for each dataset as the length of the most-parsimonious constrained tree minus the length of the most-parsimonious unconstrained tree.

[c]Includes *Gracilinanus*, *Marmosa* (sensu Gardner and Creighton, 1989), *Marmosops*, *Micoureus*, and *Thylamys*.

[d]Includes *Marmosa* (sensu Gardner and Creighton, 1989; except *M. lepida*) and *Marmosops*.

[e]The concept in current usage (Gardner, 1993).

is likewise no morphological evidence that *canescens* is closely related to *Marmosa*, which forms an unresolved mess at the base of the didelphine radiation in our nonmolecular consensus topology (fig. 17). Instead, there is strong molecular support for a clade that includes other species of *Marmosa* plus *Micoureus* (fig. 18), leaving *canescens* to participate in any of several parsimony-equivalent sister-group relationships with *Monodelphis* and higher didelphines (fig. 19). Essentially the same picture remains when the nonmolecular and IRBP data are combined (fig. 21). Removing *canescens* from *Marmosa* would therefore serve to restrict the latter name to a well-supported monophyletic group (that might or might not include *Micoureus*; see below) and to emphasize the status of *canescens* as a unique lineage that merits representation in future phylogenetic studies. Because the Linnaean convention of binomial nomenclature requires that *canescens* be provided with a recipient genus, and because no generic name is currently available for that purpose, we provide one at the conclusion of this discussion (below).

Even without *canescens*, the genus *Marmosa* remains paraphyletic in all most-parsimonious resolutions of both the IRBP and combined-data consensus topologies (figs. 18, 21). Three phylogenetically defensible alternative solutions to the current classification of these taxa merit consideration: (1) synonymizing *Micoureus* Lesson, 1842, with *Marmosa* Gray, 1821; (2) retaining *Micoureus* as a valid subgenus of *Marmosa*, for which additional subgenera would then be required to contain species that are not closely related to *murina* (the type species of *Marmosa*); or (3) retaining *Micoureus* as a genus by restricting *Marmosa* to contain only *murina* and its demonstrably close relatives, and recognizing a separate genus (or genera) for the other species. The first alternative is the simplest, but has the disadvantage of discarding a useful name for the monophyletic group that is now known as *Micoureus*. The second and third alternatives require the adoption of new or unfamiliar names, the application of which is currently hard to justify because many species of *Marmosa* remain to be analyzed. Pine (1972), for example, named the subgenus *Stegomarmosa* for *Marmosa andersoni*, but we have yet to obtain tissues from that species. The prudent course of action seems, therefore, to preserve the current generic taxonomy until future research has determined which of these arrangements is optimal. In the interim, it should be recognized that *Marmosa* is not demonstrably monophyletic, and that any biogeographic or comparative analysis based on generic membership may be suspect as a consequence.

Priorities for Future Research

The results of this study clearly demonstrate the heterogeneous contents of *Marmosa*, a traditionally recognized taxon that has been sparsely sampled in earlier phylo-

genetic analyses. Among other obvious candidates for denser sampling in future datasets is *Gracilinanus* (sensu Hershkovitz, 1992b), a genus from which one highly divergent species with ambiguous higher-level relationships has already been removed (Voss et al., 2001), but which still lacks compelling evidence of monophyly. Based on morphological character data recently compiled for another project (Voss and D.P. Lunde, in prep.), it seems likely that additional species of *Gracilinanus* will subdivide one or both of the relatively long branches that currently flank *G. microtarsus* in our combined-data consensus topology (fig. 21).

Indeed, the idea that long (well-supported) branches may be artifacts of extinction or sparse taxon sampling (Horovitz, 1999) could be used to predict where significant new phylogenetic discoveries remain to made. Among the best-supported branches in didelphid phylogeny, for example, are those subtending the didelphine radiation, the genus *Monodelphis*, and the large $2n = 22$ opossum group (clade F). Although some of the "missing links" that might occupy such long internodes are probably extinct, others may persist in the extant Neotropical fauna—either unnamed and undiscovered in some habitat neglected by collectors, or already named but yet unrecognized for what they really are.

Because the addition of more taxa will inevitably tend to further decrease phylogenetic resolution and nodal support, adding more characters to future didelphid datasets is also a priority. Among other character complexes that we have recently surveyed, the postcranial skeleton and viscera appear to be productive sources of useful new nonmolecular data, and several slowly evolving nuclear exons also seem promising. Among the latter are the Recombination Activating-1 Gene (RAG-1) and Dentin Matrix Protein-1 (DMP-1) exon 6, from each of which we have successfully amplified 1200 bp fragments that document appropriate levels of sequence divergence among several didelphid exemplars.

In view of the work that remains to be done along these lines, we think it is premature to formalize taxon definitions and diagnoses at this time. Alternative classifications of the didelphid crown group have already created a confusing array of discrepant usages for many suprageneric taxa. The names Marmosini/ae, Monodelphini/ae, and Thylamyini/ae, for example, have been differently applied by Reig et al. (1985), Hershkovitz (1992b), Kirsch et al. (1995), Kirsch and Palma (1995), and McKenna and Bell (1997), rendering those terms and their colloquial equivalents ("marmosines", etc.) effectively meaningless without a cited reference. Until evidential support converges on a stable phylogenetic hierarchy that can serve as a basis for yet another revised nomenclature, informal alphabetic labels (fig. 1) better serve the purposes of unambiguous communication.

A NEW GENUS FOR "*MARMOSA*" *CANESCENS*

For the reasons explained above, a new generic name is needed for the species hitherto known as *Marmosa canescens*. The following account fulfills the technical requirements for nomenclatural availabilty (ICZN, 1999) and summarizes relevant biogeographic observations.

Tlacuatzin, new genus

Figures 23, 24

TYPE SPECIES: *Didelphis* (*Micoureus*) *canescens* Allen, 1893, subsequently transferred to *Marmosa* by Allen (1897) and thereafter known as *Marmosa canescens* throughout the 20th century mammalogical literature (e.g., by Tate, 1933; Gardner, 1993).

GEOGRAPHIC DISTRIBUTION: Apparently endemic to Mexico, where it occurs in seasonally dry (deciduous) tropical forests from Sonora southward (principally along the Pacific littoral and adjacent slopes of the coastal cordilleras) to Oaxaca and Chiapas; isolated populations also occur in the northern part of the Yucatan Peninsula and on the Tres Marías Islands (Hall, 1981; Wilson, 1991; Reid, 1997). Armstrong and Jones (1971) implied that *T. canescens* occurs in Guatemala, but we have not examined specimens from that country, nor have we seen any published references to vouchered Guatemalan records.

CONTENTS: Only a single valid species is

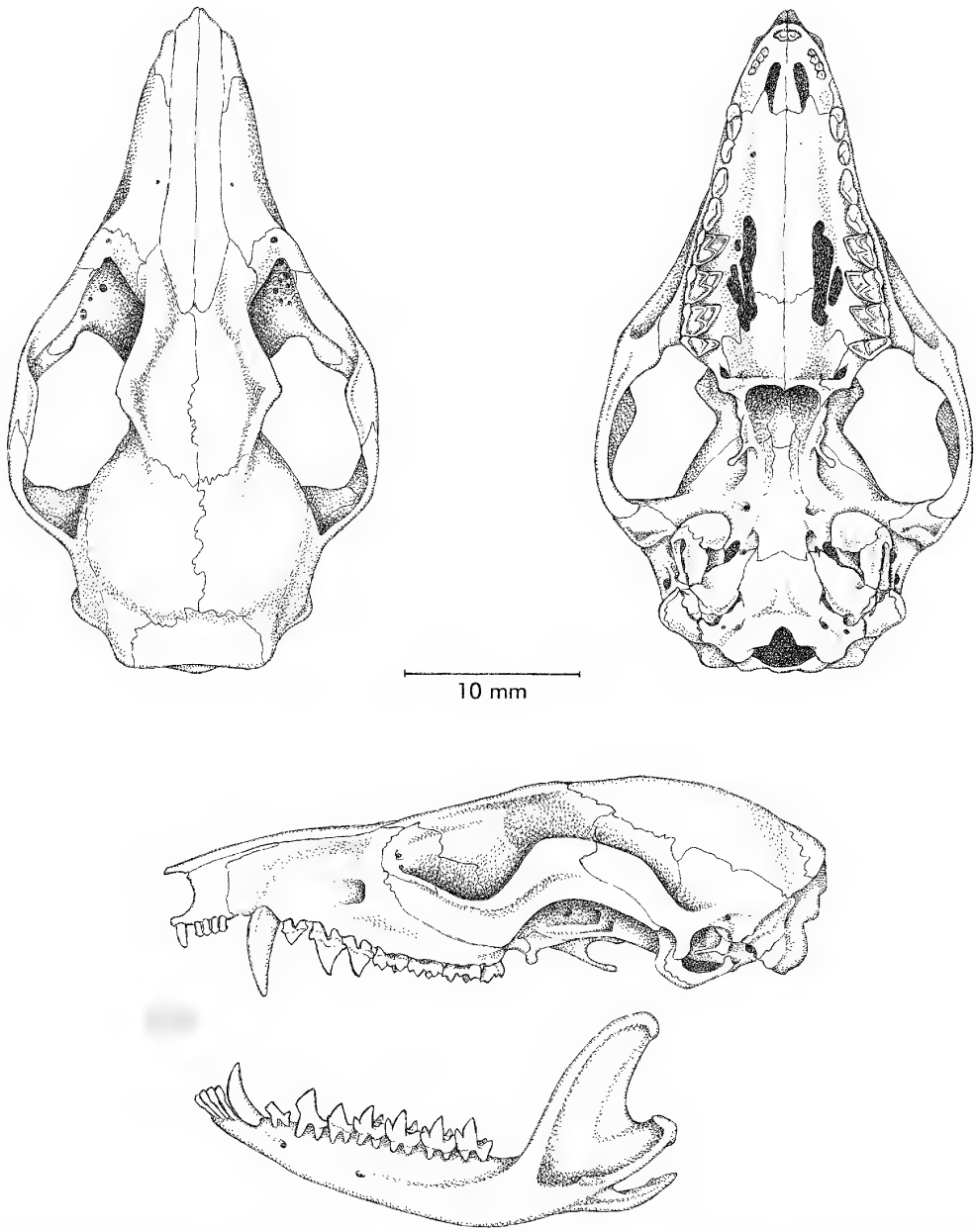


Fig. 23. Skull of *Tlacuatzin canescens*, a composite drawing based on USNM 125659 and 511261.

currently recognized following Tate (1933) and Gardner (1993), who treated *gaumeri* Osgood (1913), *insularis* Merriam (1898), *oaxacae* Merriam (1897), and *sinaloae* Allen (1898) as synonyms or subspecies of *canescens*. However, substantial geographic variation has been noted by authors (e.g., Wilson, 1991), and sufficient material (amounting to several hundred specimens in U.S. and Mexican museums) is now available for a long-overdue critical revision of these nominal taxa. Among them, the status of the Yucatecan population (*gaumeri*) merits particular attention due to its zoogeographically unusual disjunction from supposedly conspecific western Mexican forms (see Remarks, below).

ETYMOLOGY: From the Nahuatl (Aztec)

Fig. 24. *Tlacuatzin canescens*, photographed by Gerardo Ceballos in March 1995 at the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico. Specimens from southern populations (especially topotypical material from Oaxaca) are markedly grayer than this individual.

word for "opossum" (Karttunen, 1983), which is still in colloquial use as a singular masculine noun (e.g., by Villa-Ramírez, 1991).

Diagnosis and Comparisons: Small didelphines that can be distinguished from all other members of the subfamily by nonmolecular characters analyzed in this report, among which the following are salient points of morphological comparison. Rhinarium with two ventrolateral grooves; dark ocular mask present; supraocular spots absent; gular gland absent; dorsal fur unpatterned (unicolored grayish or reddish-gray), with short, inconspicuous guard hairs; manual digits III and IV subequal; large adult males with well-developed lateral carpal tubercles but not medial carpal tubercles; plantar surface of hind foot naked from heel to toes; pedal digit IV longer than other pedal digits; marsupium absent; tail essentially naked (without a conspicuously furred base), covered by epidermal scales in annular series except for distal prehensile surface, not incrassate. Rostral process of premaxillae absent; nasals conspicuously wider posteriorly than anteriorly; very large, flattened, wing-like postorbital processes present in mature adults; sagittal crest absent; parietal and alisphenoid in contact on lateral braincase; no lateral petrosal exposure through fenestra between parietal and squamosal; maxillopalatine fenestrae long (usually extending from the level of P3 to M3); palatine fenestrae absent; maxillary fenestrae present, often confluent with maxillopalatine openings; posterolateral palatal foramina posterior to M4 protocones; posterior palate with prominent lateral corners, the internal choanae constricted behind; transverse canal foramen present; secondary foramen ovale absent; ectotympanic suspension direct; fenestra cochleae exposed; paroccipital process of exoccipital small, rounded, adnate to posterior aspect of petrosal; dorsal margin of foramen magnum formed by supraocciptal and exoccipitals. Crowns of I2–I5 symmetrically rhomboidal and subequal (not increasing in size from front to back); P2 and P3 subequal in height; P3 without an anterior cutting edge; upper molars strongly dilambdodont; distinct ectoflexus present on M2 and M3 (much deeper on the latter tooth); anterior cingulum complete on M3. Distinct lingual cusp present on i1–i4; c1 an erect, dorsally recurved tooth (not procumbent and premolariform); p2 much taller than p3; dp3 with incomplete (bicuspid) trigonid; entoconid a tall sharp cusp, much higher than hypoconulid on m1, m2, and sometimes m3.

Although *Marmosa* and *Tlacuatzin* are superficially similar, *T. canescens* differs from all other species currently referred to *Marmosa* (sensu Gardner, 1993) in several nonmolecular characters that we coded for phylogenetic analysis, including: caudal scales in unambiguously annular series (character 23), absence of a premaxillary rostral process (character 29), possession of maxillary palatal vacuities (character 40), and $2n = 22$ chromosomes. Two additional comparisons also provide diagnostic criteria, but these were not coded for phylogenetic analysis due to morphological intermediates observed among other didelphine taxa. The first concerns the morphology of I2–I5, which have rhomboidal crowns that increase in breadth from front to back in *Marmosa*, such that I2 is visibly narrower than I5 in lateral view. The crowns of I2–I5 are also rhomboidal in *Tlacuatzin*, but in that taxon they do not increase in breadth from front to back, and the crowns of I2 and I5 appear subequal in lateral view. The second comparison involves the lower canine, which is a procumbent tooth with a flattened, blade-like apex and (occasionally) a small posterior accessory cusp in *Marmosa*. By contrast, c1 is an erect, simple, recurved-conical tooth in *Tlacuatzin*. Additional character-state differences (scored in appendix 5) distinguish *Tlacuatzin canescens* from *Marmosa murina* (the type species of *Marmosa*), but these are not consistently useful for generic diagnosis.

Tlacuatzin canescens resembles *Marmosa andersoni* (the type species of *Stegomarmosa* Pine, 1972) in having large postorbital processes (Pine, 1972: fig. 1), but these taxa are otherwise dissimilar. Based on our examination of the Peruvian type specimen (FMNH 84252), *M. andersoni* differs from *T. canescens* by having tail scales in spiral series; a long rostral process of the premaxillae; large palatine fenestrae; no maxillary fenestrae; upper incisor crowns that increase in breadth from I2 to I5; and a procumbent,

apically flattened c1. Unfortunately, the karyotype of *M. andersoni* is unknown. Based on these and other character data, we see no evidence for a close relationship between *T. canescens* and *M. andersoni*, and we concur with the current treatment of *Stegomarmosa* as a synonym or subgenus of *Marmosa*.

REMARKS: *Tlacuatzin canescens* is part of a distinctive fauna that inhabits dry tropical forests in western Mexico. Recent syntheses of distributional data have documented the impressive diversity of western Mexican dry forests, to which at least 25 mammalian species are endemic (Ceballos, 1995; Ceballos and García, 1995; Ceballos et al., 1998). A different fauna inhabits the dry tropical forests of the Yucatan Peninsula, however, where *T. canescens* also occurs. The Yucatecan dry forest fauna is less easily defined than that of western Mexico because dry forest on the Yucatan Peninsula grades into more mesic vegetation formations, but most Yucatecan endemics are primarily dry-forest species (e.g., *Heteromys gaumeri*, *Otonyctomys hatti*, *Mazama pandora*; see Reid, 1997; Medellín et al., 1998).

Tlacuatzin is one of seven mammalian genera endemic to Mesoamerican dry forests, the other six consisting of a shrew (*Megasorex*), one bat (*Musonycteris*), and four rodents (*Hodomys*, *Osgoodomys*, *Otonyctomys*, *Xenomys*). Without exception, all of these genera are currently considered to be monotypic (Wilson and Reeder, 1993). Whereas five are endemic to western Mexico (*Megasorex*, *Musonycteris*, *Hodomys*, *Osgoodomys*, *Xenomys*) and one is endemic to the Yucatan Peninsula (*Otonyctomys*), only *Tlacuatzin* has a disjunct distribution in both dry-forest regions. In fact, *Tlacuatzin* appears to be one of only two mammalian taxa (of any rank) endemic to Middle American dry forests that occurs both in western Mexico and the Yucatan, a biogeographic anomaly that begs critical attention.[13]

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[13] The other zoogeographically disjunct dry-forest taxon is *Cryptotis mayensis*, whose peculiar distribution was discussed by Choate (1970) and Woodman and Timm (1993).

terial that would have been ruined in less skillful hands; and Bob Randall processed enough specimen loans to have driven any normal person to New Zealand. All of the pen-and-ink illustrations in this report were drawn by Patricia Wynne, whom RSV has already thanked so often in past publications that adequate words fail him now. Eric Stiner produced the SEM images in figures 13–16.

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APPENDIX 1

Morphological Specimens Examined

The skins, skulls, and fluid-preserved material examined for this report (below) are deposited in the following collections, listed in alphabetical order by their traditional acronyms: AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); CM, Carnegie Museum of Natural History (Pittsburgh); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquizas da Amazônia (Manaus); KU, University of Kansas Museum of Natural History (Lawrence); MCZ, Museum of Comparative Zoology at Harvard University (Cambridge); MMNH, Bell Museum of Natural History (University of Minnesota, St. Paul); MNHN, Muséum National d'Histoire Naturelle (Paris); MUSM, Museo de

Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology (University of California, Berkeley); ROM, Royal Ontario Museum (Toronto); TTU, Museum of Texas Tech University (Lubbock); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); UMSNH, Universidad Michoacana de San Nicolas de Hidalgo (Morelia); USNM, National Museum of Natural History (Washington, DC); UWZM, University of Wisconsin Zoological Museum (Madison); V-, voucher collection of F. Catzeflis, Université de Montpellier (Montpellier).

Caluromys lanatus—Skins: MUSM 15290, 15291; MVZ 190248, 190249. Adult skulls: AMNH 230001, 273038, 273059; MVZ 190249, 190251. Subadult skulls: MUSM 15291. Juvenile skulls: AMNH 75913; MUSM 15290; MVZ 190248. Fluid specimens: AMNH 273038, 273059; MVZ 191185 (parous female).

Caluromys philander—Skins: AMNH 266408, 266409, 267001. Adult skulls: AMNH 266409, 267002, 267335–267337. Subadult skulls: AMNH 266408, 267332. Juvenile skulls: AMNH 96629, 96652, 267330, 267333, 267334. Fluid specimens: AMNH 266402 (parous female), 266408.

Caluromysiops irrupta—Skins: AMNH 208101; FMNH 68336; USNM 396061, 397626. Adult skulls: AMNH 208101, 244364; FMNH 60698, 84426; USNM 396061, 397626. Subadult skulls: none. Juvenile skulls: FMNH 68336, 121522. Fluid specimens: FMNH 60154, 60398.

Chironectes minimus—Skins: AMNH 164494, 264571, 264572, 266477, 266478. Adult skulls: AMNH 33027, 37483, 47190, 62365, 72020, 96759, 96760, 97319, 129704, 164494, 182939, 212909, 264572. Subadult skulls: AMNH 34197. Juvenile skulls: AMNH 16072, 126979, 127563, 128994, 264573, 266478. Fluid specimens: AMNH 24411, 150033, 266479; UMMZ 134560 (parous female).

Didelphis albiventris—Skins: AMNH 66779, 132897, 132898, 132906, 248304, 248305. Adult skulls: AMNH 132905, 132942, 248303, 248304. Subadult skulls: AMNH 66779, 132929. Juvenile skulls: AMNH 132894, 238007. Fluid specimens: AMNH 202706; UMMZ 134565–134567.

Didelphis marsupialis—Skins: AMNH 209177, 247654, 266457, 266462. Adult skulls: AMNH 266457, 266459, 266468, 266471, 266474. Subadult skulls: AMNH 266460, 266472. Juvenile skulls: AMNH 266464, 266466, 266470, 266473, 266475, 267367. Fluid specimens: AMNH 210445, 272836.

Didelphis virginiana—Skins: AMNH 90322, 139915, 146632, 180141, 180142. Adult skulls: AMNH 217749, 217762, 217772, 217775, 217786, 219223, 219224, 219231, 219234, 219235. Subadult skulls: AMNH 217750, 217782, 219868. Juvenile skulls: AMNH 217780, 217790, 219869, 219878, 240517. Fluid specimens: UMMZ 103462 (parous female), 110758, 114837 (parous female).

Glironia venusta—Skins: AMNH 71394, 71395; FMNH 41440. Adult skulls: AMNH 71394, 71395; FMNH 41440. Subadult skulls: INPA 2570. Juvenile skulls: none. Fluid specimens: INPA 2570.

Gracilinanus microtarsus—Skins: MVZ 182055, 197436. Adult skulls: MVZ 197436. Subadult skulls: MVZ 182055–182057. Juvenile skulls: none. Fluid specimens: MVZ 182054.

Lestodelphys halli—Skins: BMNH 28.12.11.207; MMNH 15708, 17171; MVZ 173727; UWZM 22422. Adult skulls: BMNH 28.12.11.207; MVZ 160109, 171069, 171070, 179180, 179182, 173727; UWZM 22422. Subadult skulls: MMNH 15708. Juvenile skulls: MMNH 17171; MVZ 17193. Fluid specimens: none.

Lutreolina crassicaudata—Skins: AMNH 133249, 133250, 143886. Adult skulls: AMNH 133249, 139825, 210420, 254512, 254513. Subadult skulls: AMNH 133255, 210419. Juvenile skulls: AMNH 210421, 210423, 210424. Fluid specimens: AMNH 202727, 235546; UMMZ 166634 (parous female); USNM 536827 (parous female).

Marmosa lepida—Skins: AMNH 67279, 182937; MNHN 1998.306; MVZ 154750. Adult skulls: AMNH 78001, 98656, 273186; KU 135118; MNHN 1998.306; MVZ 154750, 155245; USNM 461468. Subadult skulls: MNHN 1982.653; MVZ 154752. Juvenile skulls: FMNH 140824. Fluid specimens: AMNH 273186; KU 135118; MVZ 155245.

Marmosa mexicana—Skins: AMNH 12454/10763, 243700. Adult skulls: AMNH 189209, 189484, 265851; ROM 96090, 99608. Subadult skulls: AMNH 17136, 213754. Juvenile skulls: AMNH 189483, 189485. Fluid specimens: AMNH 265851 (parous female).

Marmosa murina—Skins: AMNH 273178; MUSM 15296. Adult skulls: AMNH 272816, 273062, 273063, 273140, 273178, 273188; MUSM 15293. Subadult skulls: AMNH 272870; MUSM 13283, 15294. Juvenile skulls: MUSM 15295, 15297. Fluid specimens: AMNH 268214, 272816, 273063, 273140; MUSM 15293.

Marmosa robinsoni—Skins: AMNH 36725, 36728, 37890, 147759. Adult skulls: USNM 456812, 456815, 456821, 456826, 456833. Subadult skulls: USNM 456825. Juvenile skulls: USNM 456813, 456814, 456817, 456820, 456848. Fluid specimens: UMMZ 117236, 117237.

Marmosa rubra—Skins: AMNH 71950, 71952,

71974; MVZ 153280, 153282, 153283, 154765. Adult skulls: MVZ 153280, 153282, 153283, 154765. Subadult skulls: none. Juvenile skulls: AMNH 68128, 68129; MVZ 154759. Fluid specimens: none.

Marmosops impavidus—Skins: AMNH 272760; MUSM 15298, 15299. Adult skulls: AMNH 272709, 272760, 273151; MUSM 13284, 15299, 15300. Subadult skulls: AMNH 273050. Juvenile skulls: MUSM 13285, 13286, 15306, 15307. Fluid specimens: AMNH 272709 (parous female), 273151; MUSM 13284, 15300.

Marmosops incanus—Skins: MVZ 182061, 182768, 182769; UMMZ 165662, 165663. Adult skulls: MVZ 182061, 182768–182770; UMMZ 165662, 165663. Subadult skulls: UMMZ 165661. Juvenile skulls: none. Fluid specimens: MVZ 182771, 197629.

Marmosops noctivagus—Skins: AMNH 272775, 273131; MUSM 15305. Adult skulls: AMNH 272775, 272782, 272809, 273051; MUSM 13288. Subadult skulls: MUSM 15301, 15303. Juvenile skulls: AMNH 272704, 272715; MUSM 13289–13292. Fluid specimens: AMNH 272782 (parous female), 272809, 273034, 273051 (parous female); MUSM 13288.

Marmosops parvidens—Skins: AMNH 266426, 267817. Adult skulls: AMNH 266421, 267344, 267347, 267353, 267359, 267361. Subadult skulls: AMNH 266422, 266425, 267817. Juvenile skulls: AMNH 266426, 267350, 267355. Fluid specimens: AMNH 267344 (parous female), 267348, 267353, 267359, 267361.

Marmosops pinheiroi—Skins: AMNH 266423, 267007, 267352. Adult skulls: AMNH 267340, 267342, 267345, 267346, 267349, 267352, 267357. Subadult skulls: AMNH 267007, 267356. Juvenile skulls: AMNH 266424, 267008, 267351, 267354. Fluid specimens: AMNH 267342 (parous female), 267345, 267346, 267356 (parous female), 267357.

Metachirus nudicaudatus—Skins: AMNH 266450, 267009, 267010. Adult skulls: AMNH 266435–266437, 266440, 266449, 266450, 267009, 267010. Subadult skulls: AMNH 266439, 267362. Juvenile skulls: AMNH 266451–266453, 267364. Fluid specimens: AMNH 255815, 261283, 261285; USNM 461138, 577756 (parous female).

Micoureus demerarae—Skins: AMNH 266427, 266428, 267370, 267818. Adult skulls: AMNH 266427, 266428, 266431, 266432, 267370, 267371. Subadult skulls: AMNH 266433, 267369. Juvenile skulls: AMNH 266429, 266430, 266434. Fluid specimens: AMNH 266427, 266428, 266432 (parous female).

Micoureus paraguayanus—Skins: MVZ 182063, 182064; UMMZ 165664. Adult skulls: MVZ 182063–182065; UMMZ 165664. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: MVZ 182065; UMMZ 134551.

Micoureus regina—Skins: AMNH 273164; MUSM 11063, 15316; MVZ 190323, 190332. Adult skulls: MVZ 190323, 190325, 190331, 190332. Subadult skulls: MVZ 190333. Juvenile skulls: MVZ 190324, 190328. Fluid specimens: MVZ 191201 (parous female).

Monodelphis adusta—Skins: AMNH 272695; MUSM 13297; USNM 582782, 588019. Adult skulls: AMNH 272695; MUSM 7157, 11654, 13297; USNM 582782, 588019. Subadult skulls: AMNH 272781. Juvenile skulls: none. Fluid specimens: AMNH 202650, 272781; MUSM 15318.

Monodelphis brevicaudata—Skins: AMNH 36317, 48133, 75830, 75831. Adult skulls: AMNH 257203; USNM 393438, 393439, 393441, 461435, 578009. Subadult skulls: AMNH 268061; USNM 393426, 393431. Juvenile skulls: AMNH 16953, 267744; USNM 392046, 392049, 393429, 393432, 393434, 393440, 393442, 543303, 568009. Fluid specimens: AMNH 140465, 140466, 244469.

Monodelphis emiliae—Skins: AMNH 268221; MUSM 13298; MVZ 190334; USNM 461883, 461884. Adult skulls: AMNH 268221; MUSM 13298; MVZ 190334; USNM 461883, 461884, 579574. Subadult skulls: MVZ 190335. Juvenile skulls: AMNH 95816. Fluid specimens: AMNH 95816; USNM 579574.

Monodelphis theresa—Skins: FMNH 25738; MVZ 182775. Adult skulls: FMNH 25739; MVZ 182775, 182776. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: FMNH 25739; MVZ 182776.

Philander frenata—Skins: MVZ 182066, 182067, 183246, 183247. Adult skulls: MVZ 182066, 182067, 183246. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: MVZ 182068 (parous female).

Philander mcilhennyi—Skins: AMNH 272818, 273054, 273089; MUSM 13299. Adult skulls: AMNH 272818, 273040, 273054, 273055, 273089; MUSM 13299. Subadult skulls: MVZ 190336, 190338. Juvenile skulls: AMNH 273039; MUSM 15319–15321, 15323. Fluid specimens: MUSM 15319; MVZ 191202 (parous female), 191203 (parous female).

Philander opossum—Skins: AMNH 266995, 266996, 266998, 267014. Adult skulls: AMNH 266379, 266381, 266386, 266387, 267014, 267328. Subadult skulls: AMNH 266389, 266994. Juvenile skulls: AMNH 266394, 266395, 266398, 266400, 266997. Fluid specimens: AMNH 266380, 266390.

Thylamys pallidior—Skins: AMNH 262406–262408; FMNH 54255, 162495. Adult skulls:

AMNH 262406–262408; FMNH 54255, 162495. Subadult skulls: AMNH 262405. Juvenile skulls: FMNH 51004–51006. Fluid specimens: UMMZ 156015.

Thylamys venustus—Skins: AMNH 263558, 263562; FMNH 162505. Adult skulls: AMNH 263558, 263561, 263562; FMNH 162505. Subadult skulls: AMNH 262400, 263555, 263557. Juvenile skulls: AMNH 263559, 263560. Fluid specimens: AMNH 261250, 261251.

Tlacuatzin canescens—Skins: AMNH 24896, 149104, 172128, 185769. Adult skulls: AMNH 24894, 148969, 148970; USNM 70767, 73320, 125659, 125925. Subadult skulls: AMNH 185770, 213753; USNM 37134, 70241, 96754, 508354. Juvenile skulls: AMNH 145237; USNM 70239, 70242. Fluid specimens: AMNH 144638, 165653; USNM 9514.

APPENDIX 2

New Specimens Sequenced for IRBP

The specimens newly sequenced for this report are listed below by Latin binomial, geographic origin (country, province/department/state, locality name), and museum catalog number (in parentheses; see appendix 1 for institutional acronyms). Other identifying numbers associated with samples preserved in institutional tissue collections are provided in square brackets.

Caluromys philander: French Guiana, Les Nouragues (V-823 [T-1754], V-960 [T-2020]).

Marmosa lepida: Peru, Amazonas, Huampami on Río Cenepa (MVZ 155245 [FC 4928, JLP7844]).

Marmosa mexicana: Guatemala, El Petén, Biotopo Cerro Cahui, El Ramate (ROM 99608 [FN 32277]); Guatemala, El Progresso, Río Uyús, 5 km E San Cristóbal, Acasaguascatlán (ROM 99776 [FN 34135]).

Marmosa murina: Surinam, Para, Zanderij (CM 68346 [TK 17359], 68353 [TK 17387]).

Marmosa robinsoni: Panama, Darién, Cana (TTU 39117 [TK 22552], 39118 [TK 22555]).

Marmosa rubra: Peru, Amazonas, 0.5 mi W Huampami on Río Cenepa (MVZ 153280 [JLP 6930]).

Marmosops incanus: Brazil, Minas Gerais, Estação Biologica de Caratinga, Fazenda Montes Claros, 54 km E Caratinga (MVZ 182768 [MAM 201], 182769 [MAM 202]).

Micoureus paraguayanus: Brazil, São Paulo, Fazenda Intervales, Capão Bonito (MVZ 182064 [MAM 46], 182065 [MAM 47]).

Micoureus regina: Brazil, Amazonas, Igarapé Nova Empresa, left bank Rio Juruá (MVZ 190323 [JLP 15435]); Brazil, Acre, Igarapé Porongaba, right bank Rio Juruá (MVZ 190332 [MNFS 1232]).

Monodelphis brevicaudata: Surinam, Saramacca, Raleigh Falls (CM 63511 [TK 10244]); Surinam, Nickerie, Kayserberg Airstrip (CM 68359 [TK 17069]).

Monodelphis theresa: Brazil, São Paulo, Ilha de Sebastião, Parque Estadual Ilhabela (MVZ 182776 [MAM 160]).

Philander opossum: Surinam, Para, Zanderij (CM 68365 [TK 17015]); Surinam, Suriname, Plantation Clevia, 8 km NE Paramaribo (CM 76743 [TK 17524]).

Philander frenata: Brazil, São Paulo, Fazenda Intervales, Capão Bonito (MVZ 182066 [MAM 41], 182067 [MAM 64]).

Thylamys venustus: Bolivia, Tarija, Chuquiaca (FMNH 162505 [BDP 3345]); Bolivia, Tarija, ca. 10 km by road W Narváez (FMNH 162507 [BDP 3309]).

Tlacuatzin canescens: Mexico, Jalisco, 6 km SE Chamela (TTU 37700 [TK 11826]); Mexico, Michoacan, 1 km E Playa Azul (UMSNH 2993 [TK 45085]).

APPENDIX 3

Notes on Identifications and Nomenclature

1. *Gracilinanus microtarsus*: The specimens we sequenced and those we scored for morphological characters all conform to Tate's (1933) description of the type material of this species, which we were unable to examine. Our specimens were also among those included in Costa et al.'s (2003) revisionary study of Brazilian *Gracilinanus*, wherein diagnostic characters attributed to *G. microtarsus* and *G. agilis* were correlated with cytochrome-*b* haplotype phylogenies. *Gracilinanus microtarsus* is the type species of the genus *Gracilinanus*.

2. *Marmosa mexicana*: Our molecular and morphological material of this taxon (from Mexico, Guatemala, and El Salvador) represents the nominotypical form that Tate (1933) recognized as *M. m. mexicana*.

3. *Marmosa murina*: Unpublished morphological and molecular data (Voss and Patton, in prep.) suggest that several distinct clades are represented within the geographically widespread complex of nominal taxa that have traditionally been regarded as subspecies or synonyms of *M. murina* (e.g., by Tate, 1933; Cabrera, 1958; Gardner, 1993). Although the specimens we sequenced and scored for morphological characters are referable to *M. murina* of current usage, they appear to belong to an unnamed southwestern Amazonian taxon that is distinct from the nominotypical form of northeastern Amazonia. *Marmosa murina* is the type species of the genus *Marmosa*.

4. *Marmosa robinsoni*: As currently recognized (e.g., by Gardner, 1993), *Marmosa robinsoni* includes several readily diagnosable species whose distinguishing characteristics and geographic distributions were clearly explained by Tate (1933). The material sequenced and examined for this report is referable to the taxon that Tate recognized as *M. ruatanica isthmica*, but we follow current usage pending a formal revision of the *robinsoni* group.

5. *Marmosops impavidus* and *M. noctivagus*: Our identifications of these species are based on the diagnostic morphological characters defined and illustrated by Patton et al. (2000), but we have not personally examined the type material of either taxon.

6. *Marmosops incanus*: We apply this name in the restricted sense of Mustrangi and Patton (1997), who revised the taxonomy of the southeastern Brazilian species of *Marmosops* and illustrated diagnostic cranial characters. In addition to the external characters already known to distinguish *M. incanus* from its sometimes-sympatric congener *M. paulensis* (op. cit: table 3), we observed differences in scrotal coloration (blue in *incanus*, white in *paulensis*) and carpal morphology (lateral tubercles are well developed in adult males of *incanus* but apparently not of *paulensis*) that also merit evaluation in future revisionary studies. *Marmosops incanus* is the type species of the genus *Marmosops*.

7. *Marmosops parvidens* and *M. pinheiroi*: We use these names in the restricted sense of Voss et al. (2001), who recognized several taxa formerly treated as subspecies of *parvidens* (sensu Pine, 1981) as full species and illustrated diagnostic character differences.

8. *Micoureus paraguayanus*: We are using this name for the southeastern Brazilian taxon that Patton et al. (2000) identified as *Micoureus limae*, and that Patton and Costa (2003) subsequently identified as *M. travassosi*. Although we have not examined any relevant type material, the morphological voucher material in question (the same specimens previously sequenced by Patton and his colleagues) does not conform to published descriptions of either *limae* or *travassosi*. Whereas *limae* was described by Thomas (1920) and Tate (1933) as having brownish dorsal fur, a very long (ca. 35 mm) furred tail base, and hardly any white spotting near the tail tip, MVZ 182064 and 182065 have distinctly grayish dorsal pelage, shorter (ca. 25 mm) furry tail bases, and long white tail tips. Indeed, morphological comparisons (noted by Thomas, 1920) together with new sequence data (Patton and Costa, 2003) suggest that *limae* (with type locality in Ceará) is more closely allied with Amazonian forms of *Micoureus* than with southeastern Brazilian taxa.

The identity of *travassosi* remains to be convincingly established. Unfortunately, the only published diagnosis of this taxon is in a key (Miranda-Ribeiro, 1936: 366), which clearly states that the tail is shorter than the head-and-body but provides no other useful information. Because all known species of *Micoureus* have very long tails (e.g., those of MVZ 182064 and 182064 are ca. 137–145% of head-and-body length), it is not at all clear that the current generic allocation of this taxon is correct.

Instead, *paraguayanus* appears to be the oldest available name for the grayish *Micoureus* with a conspicuously white-tipped tail that ranges from Pernambuco southward along the humid Brazilian Atlantic forest biome to eastern Paraguay. In fact, Tate's (1931) original description matches the material at hand almost perfectly. Although measurement data suggest that considerable size variation exists among referred populations of this taxon (Tate, 1933), no other identification seems appropriate in the absence of a formal revisionary study. *Micoureus cinereus* (Temminck, 1824), the type species of *Micoureus*, is an older but technically invalid synonym (Gardner, 1993).

9. *Micoureus regina*: We follow the currently accepted taxonomy (Gardner, 1993) in applying this name to the western Amazonian species for which diagnostic morphological characters were recently documented by Patton et al. (2000). However, those authors correctly noted that the type locality of *M. regina* (in the Magdalena valley of interAndean Colombia) is difficult to reconcile with this usage, and that other names for western Amazonian taxa currently treated as synonyms or subspecies (e.g., *germana* or *rutteri*) are probably more appropriate.

10. *Monodelphis brevicaudata*: We are using this name in the restricted sense of Voss et al. (2001), who recognized *M. glirina* and *M. palliolata* (formerly regarded as synonyms or subspecies of *M. brevicaudata*; see Gardner, 1993) as distinct species. *Monodelphis brevicaudata* (Erx-

leben, 1777) is the senior synonym of *M. brachyura* (Schreber, 1778), the type species of *Monodelphis*.

11. *Monodelphis theresa*: The three-striped southeastern Brazilian species of the *Monodelphis americana* complex are unrevised, and only provisional identifications can be made at present. As recognized by us, *M. theresa* is intermediate in size between the larger *M. americana* and the smaller *M. iheringi* (for differential diagnoses of the latter two species, see Thomas, 1888: 363–365). Our material of *theresa* agrees with Thomas's (1921) original description in having a domed (not flattened) dorsal cranial profile, but differs in details of pelage coloration that could be individually variable or preservational artifacts. For example, whereas Thomas (op. cit.) described the fluid-preserved BMNH holotype of *theresa* as having only faint dorsal striping, subsequently collected topotypic skins (e.g., FMNH 25738) are boldly striped like our molecular voucher (MVZ 182776). Patton and Costa (2003) used the name *theresa* for an undescribed species of three-striped *Monodelphis* recently discovered in the Peruvian Andes.

12. *Philander frenata*, *P. mcilhennyi*, and *P. opossum*: Our taxonomy for species of *Philander* follows the usages recommended by Patton and da Silva (1997). *Philander opossum* (Linnaeus, 1758) is the type species of the genus *Philander*.

13. *Thylamys pallidior* and *T. venustus*: Of the two forms of *Thylamys* currently recognized from the Bolivian highlands (Anderson, 1997), we use the name *T. pallidior* for specimens with pale gray dorsal fur, self-colored (pure white) ventral fur, small hind feet, large bullae, and no maxillary palatal vacuities. Specimens from the Bolivian highlands with darker brownish dorsal fur, gray-based yellowish ventral fur, larger hind feet, smaller bullae, and maxillary palatal vacuities are here referred to *T. venustus*. Both species have smooth interorbital regions, with no trace of postorbital processes. Our identifications are consistent with the original descriptions of both taxa (Thomas, 1902) and with subsequent accounts based on first-hand examination of the BMNH holotypes (Tate, 1933; Flores et al., 2000), but not necessarily with other published usages of these names.

APPENDIX 4

Rejected Nonmolecular Characters

We evaluated but did not use many didelphid characters described in the systematic literature. Although some of these rejected characters are discussed in our text, a discursive evaluation of all of them would occupy too much space in this preliminary report. Instead, the following list briefly summarizes the principal difficulties that we encountered with omitted external and craniodental characters analyzed in previous studies of marsupial relationships.

Body size (Kirsch and Archer, 1982: characters 46, 47; Reig et al., 1987: characters 25, 26): alternative states ("small" versus "medium" and "large") undefined, not distinct due to continuous taxonomic variation.

Presence/absence of "orbital crest" (Wroe et al., 2000: character 45): possibly synonymous with character 34 of this study, but homology uncertain.

Presence/absence of accessory posterolateral palatine foramina (Wroe et al., 2000: character 49): alternative conditions hard to recognize unambiguously; frequently polymorphic.

Condition of "alisphenoid hypotympanic sinus" (Wroe et al., 2000: character 56): unable to recognize alternative conditions coded in published data matrix from our material.

Size of alisphenoid tympanic wing in relation to other bullar components (Kirsch and Archer, 1982: characters 27, 49, 50; Reig et al., 1987: characters 28, 29; Wroe et al., 2000: character 57): alternative conditions (e.g., "poorly developed" versus "well developed") difficult to distinguish unambiguously among didelphids due to continuous range of intermediate morphologies.

Presence/absence of squamosal epitympanic recess (Kirsch and Archer, 1982: character 25): unable to replicate published taxonomic scoring from our material; apparently invariant (absent) among didelphids.

Size/extent of rostral tympanic process of petrosal (Kirsch and Archer, 1982: character 26; Sánchez-Villagra and Wible, 2002: character 7): alternative conditions (e.g., "absent or tiny" versus "small") undefined, or hard to score as unambiguous alternatives due to intermediate morphologies in this study.

Position of hiatus fallopii (Sánchez-Villagra and Wible, 2002: character 12): scoring requires specimen preparations (isolated petrosals) unavailable for most taxa in this study.

Presence/absence of postemporal sulcus on squamosal surface of petrosal (Sánchez-Villagra and Wible, 2002: character 13): scoring requires specimen preparations (isolated petrosals) unavailable for most taxa in this study.

Presence/absence of notch or foramen at pos-

terior end of postemporal sulcus (Sánchez-Villagra and Wible, 2002: character 14): alternative states difficult to distinguish unambiguously; often polymorphic.

Presence/absence of petrosal lip enclosing internal jugular vein ventrally (Wroe et al., 2000: character 61): presence/absence hard to distinguish from intermediate morphologies.

Morphology of tubal foramen (Wroe et al., 2000: character 70): alternative conditions hard to distinguish due to intermediates.

Hypsodonty of I1 (Takahashi, 1974; Archer, 1976b: character 2; Wroe et al., 2000: character 3): states not definable as unambiguous alternatives among didelphids.

Presence/absence of diastema between I1 and I2 (Archer, 1976b: character 1): invariant among didelphids (see Creighton, 1984: character 40).

Upper incisor crowns "spatulate" versus nonspatulate (Archer, 1976b: character 3; Kirsch and Archer, 1982: characters 2, 43): descriptors (e.g., "spatulate" versus "normal" or "round") undefined and unintelligible from taxonomic scoring in published matrices (see discussion under character 52).

"*Posterior [upper] incisors longer crowned than I2*" (Archer, 1976b: character 5): morphological variation difficult to score as discrete states due to morphological intermediates in this study (see discussion under character 52).

Relative size of upper canine (Archer, 1976b: character 6): states not definable as unambiguous alternatives among didelphids.

Presence/absence of diastema between P1 and "P3" [P2] (Archer, 1976b: character 16): states not unambiguously distinguishable among didelphids.

Shape of P2 and P3 (Kirsch and Archer, 1982: character 45): states ("normal" versus "bulbous") undefined, not recognizable as distinct alternatives due to continuous taxonomic variation; inconsistent with scoring in other studies using similar descriptors (see text account for our character 56).

Presence/absence or completeness of P3 cingula (Archer, 1976b: characters 13, 14; Creighton, 1984: characters 45, 46): states not unambiguously distinguishable among didelphids; often polymorphic.

Continuity of posterior cutting edge of P4 with M1 parastyle (Archer, 1976b: character 12): alternative conditions not unambiguously distinguishable.

Presence/absence, relative size, and/or connections of stylar cusps (Archer, 1976b: character 29; Kirsch and Archer, 1982: characters 12, 33, 34; Creighton, 1984: characters 50–52; Reig et al., 1987: characters 6, 7, 8; Wroe et al., 2000: character 19): putative cusp homologies (especially regarding those in C and D positions) uncertain; alternative states (especially with respect to paracrista connections to cusps A versus B) not unambiguously distinguishable, as evidenced by discrepant scoring of same taxa in different studies and/or our inability to replicate published observations.

Proportion of upper molar width to ectoloph length (Archer, 1976b: character 21): laborious to quantify; visual scoring impossible due to apparently continuous taxonomic variation.

Relative lengths of M2 and M3 (Kirsch and Archer, 1982: character 30; Reig et al., 1987: character 3): alternative conditions impossible to distinguish as unambiguous alternatives due to continuous taxonomic variation.

Relative sizes and proximity of paracones and metacones on M1–M3 (Archer, 1976b: characters 23, 26; Kirsch and Archer, 1982: characters 9, 10, 32; Creighton, 1984: character 48; Reig et al., 1987: character 5; Wroe et al., 2000: character 8): alternative states not unambiguously distinguishable due to continuous taxonomic variation; partially redundant as correlates of carnassialization (see our character 57); unable to replicate taxonomic scoring in some published data matrices.

Presence/absence/size of M4 metacone and correlated shape and size of tooth (Archer, 1976b: character 20; Kirsch and Archer, 1982: characters 7, 37; Reig et al., 1987: characters 11, 12; Wroe et al., 2000: character 9): difficult to distinguish alternative states among taxa scored for this study; correlated with carnassialization.

Shape of M3 (Kirsch and Archer, 1982: character 31; Reig et al., 1987: character 4): alternative states (based on ratio of "outer border" to "anterior border") not distinguishable as discrete alternatives due to continuous variation.

Presence/absence of protoconules and metaconules (Archer, 1976b: character 26; Kirsch and Archer, 1982: character 29; Reig et al., 1987: character 2; Wroe et al., 2000: characters 14, 15): unable to replicate published taxonomic scoring from our material; inconsistent scoring of same taxa in different published matrices; presence/absence hard to distinguish from various intermediate conditions (conules not consistently distinct in any didelphid examined).

Size of M3 protocone (Kirsch and Archer, 1982: character 11): alternative conditions ("unreduced" versus "reduced") undefined, hard to recognize unambiguously.

Shape of protocones (Kirsch and Archer, 1982: character 36; Reig et al., 1987: character 10): alternative conditions ("bulbous" versus "moderately" or "highly compressed") hard to distinguish as distinct alternatives.

Relative length metacristae of M1–M3 (Archer, 1976b: character 27; Creighton, 1984: character 49): taxonomic variation continuous, not recognizable as distinct alternative conditions among didelphids; redundant correlate of carnassialization (see our character 57).

Relative lengths of metacrista and postparacrista (Kirsch and Archer, 1982: character 35; Reig et al., 1987: character 9): taxonomic variation continuous, not divisible into unambiguously alternative states.

Orientation of m1–m3 "metacristids" [= protocristids] (Archer, 1976b: character 39; Creighton, 1984: character 57): alternative states ("oblique" versus "transverse" to long axis of toothrow) not unambiguously distinguishable.

Shape of m3 metaconid (Kirsh and Archer, 1982: character 16): shape descriptors ("transverse" versus "not transverse") problematic, not decipherable from published taxonomic scoring (unless "metaconid" lapsus for "metacristid"; see preceding character).

Relative height/size of metaconid and paraconid (Archer, 1976b: character 38; Kirsch and Archer, 1982: character 41; Reig et al., 1987: character 17): unable to replicate published taxonomic scoring from our material; invariant among didelphids (unworn metaconid always higher/larger than paraconid).

Relative size/height protoconid and paraconid (Kirsch and Archer, 1982: character 42; Reig et al., 1987: character 18): states not well defined, not recognizable as distinct alternatives due to continuous taxonomic variation; unable to replicate published taxonomic scoring from our material.

Relative lengths trigonid and talonid (Kirsch and Archer, 1982: character 39; Reig et al., 1987: character 15): taxonomic variation continuous, not divisible into unambiguously alternative states.

Number of cusps on m4 talonid (Archer, 1976b: character 35; Kirsch and Archer, 1982: character 19; Creighton, 1984: character 56; Wroe et al., 2000: character 44): alternative states not unambiguously distinguishable (presence/absence/indistinctness of very small cusps hard to score); polymorphic in most taxa with narrow (laterally compressed) talonids.

Size of m3 talonid (Kirsch and Archer, 1982: character 20): alternative states ("normal" versus "reduced") undefined, not unambiguously distinguishable in our material.

Size/shape of m4 talonid (Kirsch and Archer, 1982: character 40; Reig et al., 1987: character 16): taxonomic variation continuous, not divisible into unambiguous alternative states.

Shape of m2–m4 talonids (Reig et al., 1987: character 13): states (defined in terms of ratio of talonid width to talonid length) not distinguishable as distinct alternatives due to continuous taxonomic variation.

Relative size/shape of m3 and m4 (Kirsch and Archer, 1982: character 38; Reig et al., 1987: character 14; Wroe et al., 2000: character 42): unable to replicate taxonomic scoring in published data matrices from our material; alternative conditions not unambiguously distinguishable.

Completeness/size of labial cingula on lower molars (Archer, 1976b: character 41; Reig et al., 1987: character 19; Wroe et al., 2000: character 36): alternative conditions not unambiguously distinguishable.

APPENDIX 5

Nonmolecular Data Matrix

The matrix of nonmolecular characters analyzed in this report is reproduced below. An electronic version of the same data in Nexus format can be downloaded from ftp://ftp.amnh.org/pub/mammalogy.

Caluromys lanatus: 01100 00002 00020 01100 00211 00011 00010 00000 00000 11000 11010 00100 00000 00000 0

Caluromys philander: 01100 00002 00020 01000 10201 00011 00010 00000 00000 11000 11010 00100 00000 00000 0

Caluromysiops irrupta: 000–0 02002 00020 01?00 00211 00001 00011 00000 00002 11000 11010 00000 00000 01??? ?

Chironectes minimus: 10120 01000 20021 01201 11200 00000 01021 00200 01012 10101 00002 11111 21000 00111 1

Didelphis albiventris: 10100 00110 00010 01100 11201 00000 01021 00210 01012 10110 01002 11111 21000 00111 1

Didelphis marsupialis: 10100 00110 00020 01100 11201 00000 01021 00210 01012 10110 01002 11111 21000 00111 1

Didelphis virginiana: 10100 00110 00010 01100 11201 00000 01021 00210 01012 10110 01002 11111 21000 00111 1

Glironia venusta: 00100 ?0001 0??20 00–00 00–11 ??000 00010 00100 00010 00000 01001 01110 000?0 00??? ?

Gracilinanus microtarsus: 00100 10001 0??20 00–10 20001 00010 00000 02211 01011 00000 00001 11210 000?0 00000 0

Lestodelphys halli: 10100 16000 10000 10–10 20000 ?0100 00000 01210 11011 01000 00002 11211 00211 00000 0

Lutreolina crassicaudata: 100–0 00000 00000 01200 11200 10000 01021 00210 01212 10110 01002 11111 21000 00111 1

Marmosa canescens: 00100 00001 01020 00–00 20001 00000 00010 00201 01010 00000 00001 11210 00010 00111 1

Marmosa lepida: 00100 00001 01020 00–00 20201 00010 00010 00200 01010 00000 00101 11210 00010 00??? ?

Marmosa mexicana: 00100 10001 01120 00–00 20101 00010 00010 00210 01010 00000 00001 11210 00010 00000 0

Marmosa murina: 00100 00001 00020 00–00 20201 00010 00010 00200 01010 00000 00001 11210 00010 00000 0

Marmosa robinsoni: 00100 10001 01120 00–00 20101 00010 00010 00200 01010 00000 00001 11210 00010 00000 0

Marmosa rubra: ?0100 00001 01120 00–0? 20201 00010 00000 00200 01010 01000 00001 11210 00010 00??? ?

Marmosops impavidus: 00100 00000 01020 00–00 20201 01010 00000 02210 01011 00000 00001 11211 00000 00000 0

Marmosops incanus: 00100 10000 01020 00–10 20201 010?0 00100 01210 01011 00000 00001 11211 000?0 00000 0

Marmosops noctivagus: 00100 10000 01020 00–00 20201 01010 00000 01210 01011 00000 00001 11211 00000 00000 0

Marmosops parvidens: 00100 00000 01020 00–00 20201 01010 00000 02200 01011 00000 00201 11210 00000 00??? ?

Marmosops pinheiroi: 00100 00000 01020 00–00 20201 01010 00000 02200 01011 00000 00201 11211 00000 00??? ?

Metachirus nudicaudatus: 10121 10000 00020 00–00 20100 00000 00000 10200 01011 00110 00001 11211 10000 00000 0

Micoureus demerarae: 00100 00001 01120 00–00 20201 00010 00010 00200 01010 00000 00001 11210 00010 00000 0

Micoureus paraguayanus: 00100 00001 01120 00-?0 10201 00010 00010 00200 01010 00000 00001 11210 ?00?0 00000 0

Micoureus regina: 00100 00001 01120 00–00 20201 00010 00010 00200 01010 00000 00001 11210 00010 00000 0

Monodelphis adusta: 100–0 10000 00000 00–00 20000 00000 10000 00200 01210 00000 00002 11211 001?1 10??? ?

Monodelphis brevicaudata: 100–0 14000 00000 00–00 00000 00000 10000 00200 01210 00000 00002 11211 10101 10010 1

Monodelphis emiliae: 100–0 15000 00000 00–00 00000 00000 10000 00200 01210 01000 00002 11211 ?0201 10010 1

Monodelphis theresa: 100–0 03000 00000 0???0 20000 00000 10000 00200 01212 00000 00002 11211 ?01?1 10??? ?

Philander frenata: 10111 00000 00020 01100 11201 10000 01021 00210 01012 10110 01002 11111 ?10?0 00111 1

Philander mcilhennyi: 10121 00000 00020 01100 11201 10000 01021 00210 01012 10110 01002 11111 21000 00111 1

Philander opossum: 10121 00000 00020 01100 11201 10000 01021 00210 01012 10110 01002 11111 21000 00111 1

Thylamys pallidior: 10100 16000 10020 1???0 20001 00100 00100 02210 11011 01000 00002 11211 00110 00000 0

Thylamys venustus: 00100 16000 10020 1???0 20001 00100 00100 02211 11011 01000 00002 11211 00110 00000 0